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The Feeding Ecology of Some Zooplankters That are Important Prey Items of Larval Fish

Jefferson T. Turner

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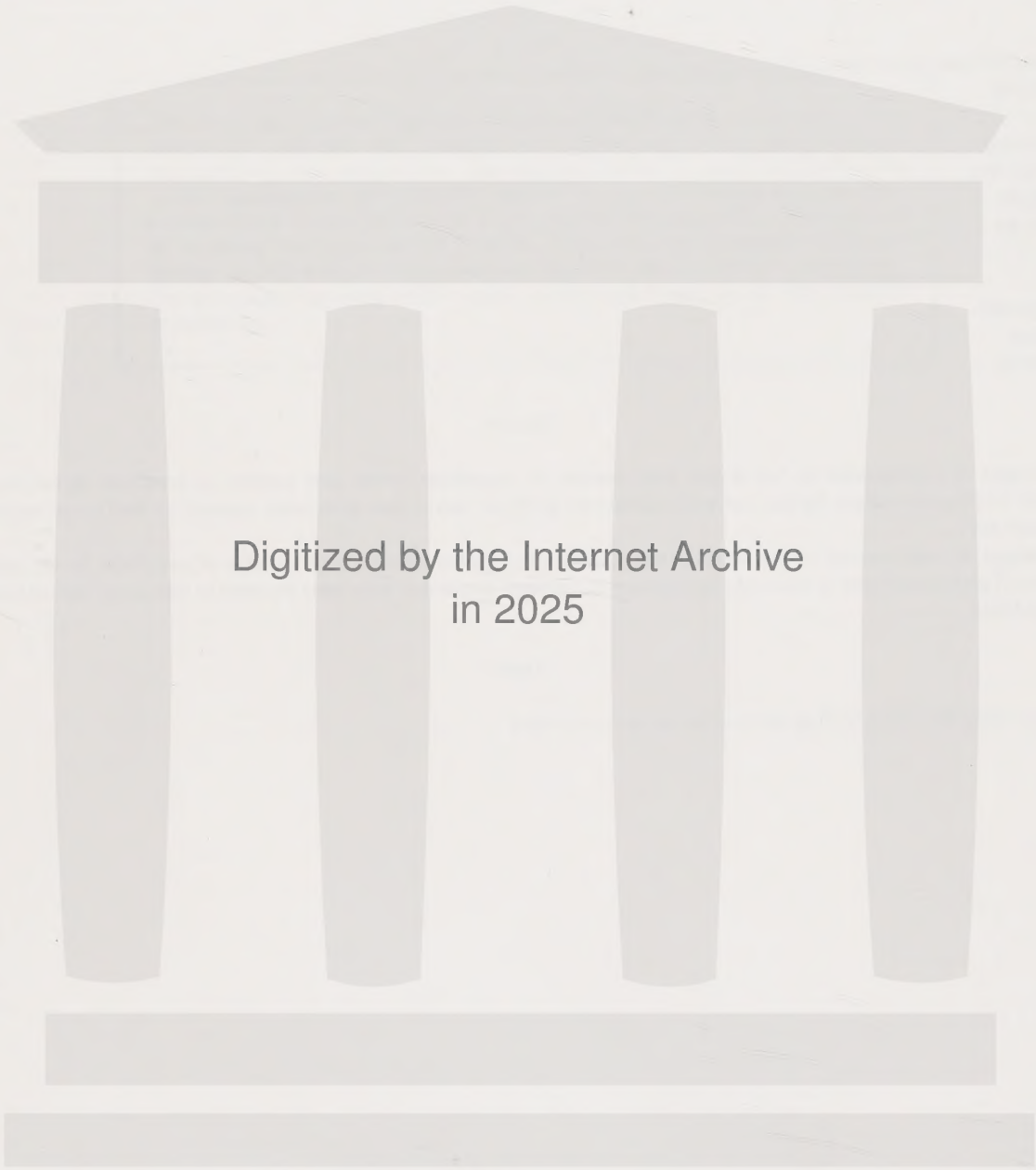

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The Feeding Ecology of Some Zooplankters That are Important Prey Items of Larval Fish[1]

JEFFERSON T. TURNER [2]

ABSTRACT

Diets of 76 species of fish larvae from most oceans of the world were inventoried on the basis of information in 40 published studies. Although certain geographic, size- and taxon-specific patterns were apparent, certain zooplankton taxa appeared in the diets of larvae of a variety of fish species in numerous localities. Included were six genera of calanoid copepods *(Acartia, Calanus, Centropages, Paracalanus, Pseudocalanus, Temora),* three genera of cyclopoid copepods *(Corycaeus, Oithona, Oncaea),* harpacticoid copepods, copepod nauplii, tintinnids, cladocerans of the genera *Evadne* and *Podon,* barnacle nauplii, gastropod larvae, pteropods of the genus *Limacina,* and appendicularians. Literature on feeding habits of these zooplankters reveals that most of the copepods are omnivorous, feeding upon both phytoplankton and other zooplankton. Some taxa, such as *Calanus, Paracalanus, Pseudocalanus,* and copepod nauplii appear to be primarily herbivorous, while others, such as *Acartia, Centropages, Temora,* and cyclopoids exhibit broad omnivory or carnivory. The noncopepod zooplankters are primarily filter-feeders upon phytoplankton and/or bacterioplankton. Despite the importance of zooplankters in larval fish food webs, specific knowledge of the feeding ecology of many taxa is poor. Further, much present knowledge comes only from laboratory investigations that may not accurately portray feeding habits of zooplankters in nature. Lack of knowledge of the feeding ecology of many abundant zooplankters, which are also important in larval fish food webs, precludes realistic understanding of pelagic ecosystem dynamics.

INTRODUCTION

It has long been thought that fluctuations in year class sizes are largely dependent upon the success of fish larvae in finding necessary kinds and amounts of food (Hjort 1914). Understanding the dynamics of food webs that support fish larvae requires information not only on the kinds and amounts of food required by larval fish, but also of the organisms upon which larvae feed. Although larvae of numerous fish species, particularly clupeoids, feed directly on phytoplankton (Blaxter 1974; Lasker 1975, 1978, 1981; Mendiola 1969, 1974), most also feed upon zooplankton, at least during some stage of larval life. Since larvae of numerous species of fish may feed selectively upon certain zooplankters, which in turn may feed selectively on certain phytoplankters, there is a possiblity that climatic- or anthropogenic-induced alteration of phytoplankton species assemblages may produce changes in food chain structures which extend to the top (Greve and Parsons 1977).

Since many of the thousands of zooplankton taxa present in the sea may not be directly involved in larval fish food webs, it is important to identify those zooplankters which are the food of larval fish. The feeding habits of these zooplankters must then be defined before food webs of larval fish can be understood.

This paper reviews existing knowledge of feeding habits of zooplankters that are important forage items of larval fish. These zooplankters were identified from 40 published studies inventorying the diets of 76 species of fish larvae from most oceans of the world. Eleven clupeiform, 38 perciform, 15 pleuronectiform, and 12 gadiform species were represented (Table 1). Care was taken to use information on feeding of larvae only, not postlarvae.[3] All but a few studies were based on examinations of gut contents of field-caught larvae; the few exceptions were based on studies of larvae feeding upon natural zooplankton assemblages. Collette (1978), Hureau and Monod (1973), and Robins et al. (1980) were used to identify taxonomic synonymies of fish species.

Lists of fish species whose larvae have been reported to eat various zooplankton taxa are presented in Appendix Tables 1-20. For zooplankton taxa eaten by larvae of >5% of the total 76 fish species, the percentages of the total number of fish, as well as percentages of the total number from each order (Clupeiformes, Perciformes, Pleuronectiformes, and Gadiformes) that eat various zooplankters, are presented in Figures 1 and 2.

Certain geographic, size-specific, or taxon-specific patterns are apparent from these figures. For instance, the cold-water copepods *Calanus* and *Pseudocalanus* are consumed mainly by cold-water cod larvae (Gadiformes). Conversely, the apparent low utilization of the copepod genera *Corycaeus, Oncaea,* and *Microsetella,* which are most abundant in tropical waters, is probably a reflection of fewer studies of the feeding of tropical fish larvae than of temperate fish larvae. Although copepod nauplii are eaten by larvae of most species, and by larvae of all clupeoid species examined, they appear to be utilized much more intensively by younger (smaller) larvae. Since many clupeoid larvae are known to feed directly on phytoplankton, it is no surprise that most also eat small items such as copepod nauplii and tintinnids. Although appendicularians were eaten by only a small percentage of larvae, they were an important food for many temperate flatfish larvae (Pleuronectiformes). Further, since appendicularians are dominant zooplankters throughout the year, mainly in oceanic

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[3]It is clear from sizes of fish examined that Lebour's (1918, 1919, 1920) papers dealt with what we now call larvae. Apparently, larvae in her classification referred to those which still retained a yolk sac.

Table 1.—Species of fish for which the feeding habits of larvae were examined.

Species	Common name	Location[1]	References
		Order Clupeiformes (herring-like fishes)	
Anchoa mitchelli	bay anchovy	FLAE	Detwyler and Houde (1970)
Brevoortia patronus	gulf menhaden	GOMEX	Govoni et al. (1983)
Brevoortia tyrannus	Atlantic menhaden	NCE	Kjelson et al. (1975)
Brevoortia tyrannus	Atlantic menhaden	DELE	June and Carlson (1971)
Clupea harengus	herring	NWECW	Bainbridge and Forsyth (1971)
Clupea harengus	herring	NWECW	Bjørke (1971, 1978)
Clupea harengus	herring	NWECW	Blaxter (1965)
Clupea harengus	herring	NWECW	Bowers and Williamson (1951)
Clupea harengus	herring	NWECW	Gamble et al. (1981)
Clupea harengus	herring	NWECW	Lebour (1918, 1919, 1920, 1921)
Clupea harengus	herring	NWECW	Ogilvie (1927)
Clupea harengus	herring	GOM	Sherman and Honey (1971)
Clupea harengus	herring	BOF	White (1977, 1980)
Engraulis anchoita	Argentine anchovy	ACW	Ciechomski (1967)
Engraulis mordax	northern anchovy	CALCW	Arthur (1976)
Engraulis ringens	Peru anchovy	PCW	Mendiola (1974)
Harengula pensacolae	scaled sardine	FLAE	Detwyler and Houde (1970)
Sardina pilchardus (*Clupea pilchardus*)[2]	pilchard	NWECW	Lebour (1920, 1921)
Sardinops sagax	California sardine	CALCW	Arthur (1976)
Sprattus sprattus (*Clupea sprattus*)[2]	sprat	NWECW	Lebour (1918, 1919, 1920, 1921)
		Order Perciformes (spiny-rayed fishes)[3]	
Agonus cataphractus	armed bullhead	NWECW	Lebour (1918, 1919, 1920)
Ammodytes americanus	sand lance	NEE	Covill (1959)
Ammodytes marinus	sand lance	NWECW	Ryland (1964); Wyatt (1974)
Ammodytes tobianus (*Ammodytes lanceolatus*)[2]	sand lance	NWECW	Lebour (1918, 1920)
Auxis sp.	frigate tuna	INDO	Uotani et al. (1981)
Blennius gattorugine	blenny	NWECW	Lebour (1918, 1919)
Callionymus lyra	dragonet	NWECW	Lebour (1918, 1919, 1920)
Coryphoblennius galerita (*Blennius galerita*)[2]	blenny	NWECW	Lebour (1918, 1919)
Crystallogobius nilssoni	gobi	NWECW	Lebour (1918, 1919, 1920)
Ctenolabrus rupestris	wrasse	NWECW	Lebour (1919, 1920)
Cyclogaster montagui	sea snail	NWECW	Lebour (1918, 1919)
Diplecogaster bimaculatus (*Lepadogaster bimaculatus*)[2]	clingfish	NWECW	Lebour (1919, 1920)
Eutrigla gurnardus (*Trigla gurnardus*)[2]	gurnard	NWECW	Lebour (1918, 1920)
Gobius niger (*Gobius paganellus*)[2]	goby	NWECW	Lebour (1919, 1920)
Gobiusculus flavescens (*Gobius minutus*)[2] (*Gobius ruthensparri*)[2]	goby	NWECW	Lebour (1918, 1919, 1920)
Katsuwonus pelamis	skipjack tuna	INDO	Uotani et al. (1981)
Labrus bergylta	wrasse	NWECW	Lebour (1918, 1919, 1920)
Labrus bimaculatus (*Labrus mixtus*)[2]	wrasse	NWECW	Lebour (1920)
Lagodon rhomboides	pinfish	NCE	Kjelson et al. (1975)
Leiostomus xanthurus	spot	NCE	Kjelson et al. (1975)
Leiostomus xanthurus	spot	GOMEX	Govoni et al. (1983)
Lepadogaster candollei	clingfish	NWECW	Lebour (1918, 1919, 1920)
Lepadogaster lepadogaster (*Lepadogaster gouani*)[2]	clingfish	NWECW	Lebour (1918, 1919)
Micropogonias undulatus	Atlantic croaker	GOMEX	Govoni et al. (1983)
Myoxocephalus aenaeus	sculpin	NEE	Laroche (1982)
Myoxocephalus octodecemspinosus	sculpin	NEE	Laroche (1982)
Myoxocephalus scorpius	sculpin	NEE	Laroche (1982)
Pomatoschistus microps (*Gobius microps*)[2]	goby	NWECW	Lebour (1920)
Sebastes marinus	redfish	IS	Bainbridge (1965)
Sebastes marinus	redfish	GOM	Marak (1974)
Scomber scomber	mackerel	NWECW	Lebour (1918, 1920)
Taurulus bubalis (*Cottus bubalis*)[2]	bullhead	NWECW	Lebour (1918, 1919, 1920)
Thunnus alalunga	albacore	INDO	Uotani et al. (1981)
Thunnus albacares	yellowfin tuna	INDO	Uotani et al. (1981)

Table 1.—*Continued.*

Species	Common name	Location[1]	References
Thunnus maccoyii	southern bluefin	INDO	Uotani et al. (1981)
Thunnus obesus	bigeye tuna	INDO	Uotani et al. (1981)
Trachinus vipera	weaver	NWECW	Lebour (1918, 1919, 1920)
Trachurus symmetricus	jack mackerel	CALCW	Arthur (1976)
Trachurus trachurus (*Caranx trachurus*)[2]	horse mackerel	NWECW	Lebour (1918, 1919, 1920)
Triglops murrayi	sculpin	NEE	Laroche (1982)
	Order Pleuronectiformes (flatfish)		
Arnoglossus sp.	lefteye flounder	NWECW	Lebour (1918, 1920)
Limanda limanda (*Pleuronectes limanda*)[2]	dab	NWECW	Last (1978a); Lebour (1918, 1919, 1920)
Microchirus variegatus (*Solea variegata*)[2]	thickback sole	NWECW	Lebour (1918, 1919)
Microstomus kitt (*Pleuronectes microcephalus*)[2]	lemon dab	NWECW	Lebour (1918, 1919, 1920)
Phrynorhombus regias (*Zeugopterus unimaculatus*)[2]	turbot	NWECW	Lebour (1918)
Phrynorhombus norvegicus (*Scophthalmus norvegicus*)[2]	turbot	NWECW	Lebour (1918, 1920)
Platichthys flessus (*Pleuronectes flessus*)[2]	righteye flounder	NWECW	Last (1978a); Lebour (1918, 1920)
Pleuronectes platessa	plaice	NWECW	Last (1978a); Lebour (1920); Ryland 1964; Shelbourne (1953, 1957, 1962); Wyatt (1974)
Psetta maxima (*Rhombus maximus*)[2]	turbot	NWECW	Lebour (1920)
Pseudopleuronectes americanus	winter flounder	NEE	Pearcy (1962)
Scophthalmus maximus	turbot	NWECW	Last (1979)
Scophthalmus rhombus (*Rhombus laevis*)[2]	brill	NWECW	Lebour (1919, 1920)
Solea nasuta (*Solea lascaris*)[2]	lemon sole	NWECW	Lebour (1918, 1919, 1920)
Solea solea (*Solea vulgaris*)[2]	common sole	NWECW	Last (1978a); Lebour (1918, 1919, 1920)
Zeugopterus punctatus	turbot	NWECW	Lebour (1918)
	Order Gadiformes (cod-like fishes)		
Ciliata mustela (*Onos mustela*)[2]	rockling	NWECW	Lebour (1918, 1919, 1920)
Gadus morhua	cod	NWECW	Last (1978b); Lebour (1918); Ellertsen et al. (1981)
Gadus morhua	cod	GOM	Marak (1960); Sysoeva and Degtereva (1965)
Melanogrammus aeglefinus	haddock	NWECW	Ogilvie (1938)
Melanogrammus aeglefinus	haddock	GOM	Marak (1960)
Merlangius merlangus (*Gadus merlangus*)[2]	whiting	NWECW	Last (1978b); Lebour (1918, 1919, 1920)
Merluccius merluccius	hake	NWECW	Lebour (1920)
Merluccius productus	Pacific hake	CALCW	Sumida and Moser (1980)
Micromesistius poutassou	blue whiting	NWECW	Conway (1980)
Molva molva	ling	NWECW	Lebour (1920)
Pollachius pollachius (*Gadus pollachius*)[2]	pollack	NWECW	Lebour (1918, 1919, 1920)
Pollachius virens	coalfish	GOM	Marak (1960)
Trisopterus luscus (*Gadus luscus*)[2]	bib	NWECW	Last (1978b); Lebour (1918, 1919, 1920)
Trisopterus minutus (*Gadus minutus*)[2]	bib	NWECW	Lebour (1918, 1920)

[1]ACW, Argentine coastal waters; BOF, Bay of Fundy; CALCW, California coastal waters; DELE, Delaware estuarine waters; FLAE, Florida estuarine waters; GOM, Gulf of Maine; GOMEX, Gulf of Mexico coastal waters; INDO, Indian Ocean; IS, Irminger Sea; NCE, North Carolina estuarine waters; NEE, New England estuarine waters; NWECW, northwest European coastal waters; PCW, Peru coastal waters.

[2]Previous taxonomic synonymy.

[3]For the purposes of this review, five species of Order Scorpaenidae (*Myoxocephalus aenaeus, M. octodecemspinosus, M. scorpius, Sebastes marinus,* and *Triglops murrayi*) are included with the perciforms, since their larvae are morphologically and ecologically "perciform-like."

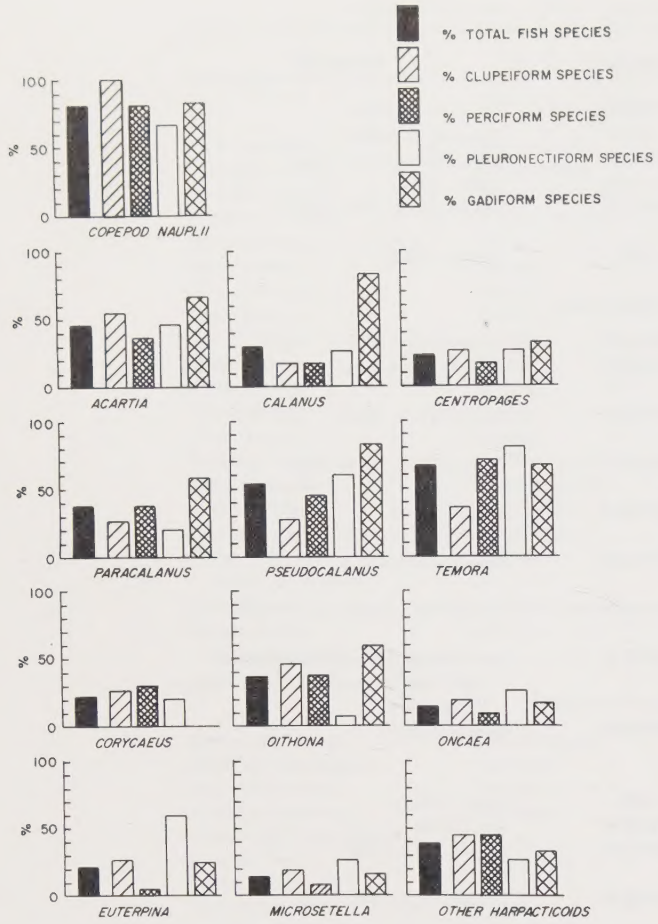

Figure 1.—Percentages of the total number of fish larvae (76 species), the total number of clupeiform larvae (11 species), the total number of perciform larvae (38 species), the total number of pleuronectiform larvae (15 species), and the total number of gadiform larvae (12 species), listed in Table 1, that have been reported to feed upon various copepod taxa.

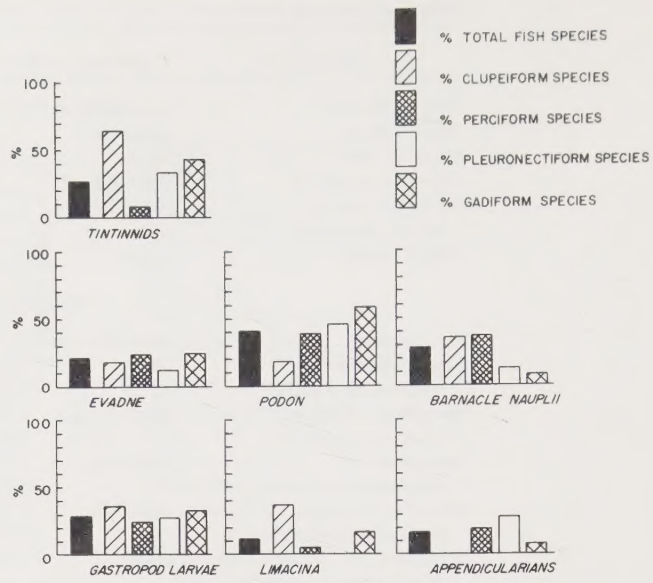

Figure 2.—Percentages of the total number of fish larvae (76 species), the total number of clupeiform larvae (11 species), the total number of perciform larvae (38 species), the total number of pleuronectiform larvae (15 species), and the total number of gadiform larvae (12 species), listed in Table 1, that have been reported to feed upon various noncopepod taxa.

waters, it is understandable that they were important prey items for oceanic tuna larvae (Perciformes).

Aside from such specific patterns, it is clear that the zooplankton taxa shown in Figures 1 and 2 are eaten by larvae of a variety of fish species in numerous localities. These zooplankters include adults and/or copepodites of six genera of calanoid copepods (*Acartia, Calanus, Centropages, Paracalanus, Pseudocalanus,* and *Temora*), adults and/or copepodites of three genera of cyclopoid copepods (*Corycaeus, Oithona,* and *Oncaea*), and adults and/or copepodites of two genera of planktonic harpacticoid copepods (*Euterpina* and *Microsetella*). Also included are zooplankton often unidentified, such as harpacticoids, copepod nauplii (some of which were identified to genus, but most not), tintinnids, the cladocerans *Evadne* and *Podon,* barnacle nauplii, gastropod larvae, the pteropod *Limacina,* and appendicularians. However, with the exception of the appendicularians which were not identified in the study of Uotani et al. (1981), the other records for appendicularians refer to *Oikopleura dioica* and *Frittilaria borealis.*

The remainder of this review will summarize published knowledge of feeding habits of the zooplankton taxa listed above.

ACARTIA

Acartia is a broadly distributed copepod genus (Bradford 1976). In most estuarine waters of the world one or more *Acartia* species are numerically co-dominant, if not the dominant, copepods (see references cited in Turner 1981).

Acartia is omnivorous. Early gut content studies reveal remains of diatoms, dinoflagellates, radiolarians, and crustaceans (Lebour 1922; Marshall 1949; Conover 1956). Numerous laboratory studies have shown that various species of *Acartia* feed upon unialgal or mixed cultures of diatoms, dinoflagellates, microflagellates, coccolithophorids, and other phytoplankton (Gauld and Raymont 1953; Conover 1956, 1960; Anraku and Omori 1963; Anraku 1964a, b; Marshall and Orr 1966; Esaias and Curl 1972; Gaudy 1974; Corkett and Zillioux 1975; Nival and Nival 1976; O'Connors et al. 1976; Piontkovskii and Petipa 1976; Reeve and Walter 1977; Dagg 1977; Roman 1977; Honjo and Roman 1978; Tomasini and Mazza 1978; Donaghay and Small 1979a, b; White 1979; Deason 1980a, b; Rosenberg 1980; White 1981; Cahoon 1981; Bartram 1981; Tomas and Deason 1981; Weiss 1983).

Acartia is also capable of carnivorous feeding. Various species of *Acartia* eat their own juveniles (Conover 1956; Roman 1977; Landry 1978; Lonsdale et al. 1979), nauplii of other copepod species (Hodgkin and Rippingale 1971; Rippingale and Hodgkin 1975; Lonsdale et al. 1979; Lonsdale 1981), *Artemia* nauplii[4] (Conover 1960; Anraku and Omori 1963; Gaudy 1974), juvenile chaetognaths (Davis 1977), and tintinnids (Turner and Anderson in press; Robertson 1983).

[4]The use of *Artemia* nauplii as prey in experiments on predation by marine zooplankton is artificial since *Artemia* is absent from the ocean. References to such studies will be included, however, since ingestion of *Artemia* nauplii is the only evidence of feeding upon animal prey by some marine zooplankters.

In addition to eating phytoplankton and zooplankton, *Acartia* eats other items. Friedman (1980) presented electron microscopic evidence that *A. tonsa* can ingest bacteria as small as 0.5 μm in diameter. It can also ingest particulate macrophyte detritus, but does not survive well on this diet (Roman 1977). *Acartia negligens* collected near coral reefs ingested and assimilated up to 50% of the organic matter in mucus produced by scleractinian corals (Richman et al. 1975).

The few attempts to compare the relative importance of plant and animal food for *Acartia* have produced mixed results. Anraku and Omori (1963) found that *A. tonsa* ate equal amounts of *Artemia* nauplii and the diatom *Thalassiosira fluviatilis.* However, Gaudy (1974) reported that *A. clausi* exhibited a marked preference for phytoplankton over *Artemia* nauplii. Lonsdale et al. (1979) demonstrated that the rates of predation by *A. tonsa* adults on conspecific nauplii and nauplii of other copepods were not reduced by the presence of alternative phytoplankton food.

There is also disagreement on the selective feeding of *Acartia* on particles. Although many studies have suggested size-selective grazing upon the largest available cells in algal cultures, recent studies of the feeding of *Acartia* on naturally occurring particulate assemblages (Hargrave and Geen 1970; Richman et al. 1977; Poulet 1978; Mayzaud and Poulet 1978; Roman and Rublee 1980; Ryther and Sanders 1980; Bartram 1981; Turner and Anderson 1983) have produced contradictory results. Richman et al. (1977) found that *A. tonsa* and *A. clausi* preferentially fed upon the largest available particles, even if these were not the most abundant. However, as these larger particles were grazed down, grazing pressure shifted to biomass peaks of smaller sized particles. Poulet (1978) and Mayzaud and Poulet (1978) concluded that *A. clausi* was an opportunistic grazer on particles between 1.5 and 150 μm equivalent spherical diameter, and feeding was nonselective with regard to particle size. As in the study of Richman et al. (1977), Poulet (1978) reported that grazing *A. clausi* tracked biomass peaks. Turner and Anderson (1983) found that in terms of filtration rate, *A. hudsonica* (= *A. clausi*) was unselective when feeding upon combinations of naturally occurring concentrations of a small dinoflagellate (*Heterocapsa triquetra*) and a larger dinoflagellate (*Gonyaulax tamarensis*), or *G. tamarensis* and tintinnids. Each type of food was eaten in approximate proportion to its availability. Ryther and Sanders (1980) examined the feeding of *A. tonsa* on natural particulate assemblages in large-volume continuous-flow enclosures and reported that *A. tonsa* reduced the number of centric diatoms (mainly *Skeletonema costatum*) by 10% in grazed enclosures, but that small flagellates increased by 35-60%. Presumably this occurred because, as suggested by Conover (1956), *Acartia* is an inefficient grazer of small flagellates, and these increased in the grazed enclosures due to reduced nutrient competition with diatoms.

Other studies suggest that some flagellates are poor food for *Acartia.* Tomas and Deason (1981) offered *A. hudsonica* and *A. tonsa* cultures of the diatom *Skeletonema costatum* and the flagellates *Dunaliella tertiolecta* and *Olisthodiscus luteus,* either singly or in combination. At intermediate and high concentrations, *O. luteus* was inhibitory to feeding, both on itself and on the other phytoplankters. Also, Parrish and Wilson (1978) found that *A. tonsa* females produced eggs equally well on diets of the diatom *Thalassiosira pseudonana* or the "large" (100-140 μm^3) flagellate *Chroomonas salina,* but that when the small flagellate *Isochrysis galbana* (40 μm^3) was the only food, egg production ceased, as with starved females, after 3 d.

These observations are somewhat at odds with the results of *Acartia* culture studies. Flagellates such as *Isochrysis galbana, Dunaliella tertiolecta,* and *Platymonas succia* have been used as food (usually in combination with diatoms) to rear multiple generations of *A. tonsa, A. clausi,* or *A. steueri* from fertilized egg to adult (Zillioux and Wilson 1966; Heinle 1969, 1970; Zillioux 1969; Nassogne 1970; Uye 1980a, b,, 1981; Tester 1982). However, Klein Breteler (1980) successfully cultured *A. clausi* only when dinoflagellates were added as food, not when microflagellates alone were used. These discrepancies possibly reflect the suitability of small flagellates as food for *Acartia* nauplii, but additional diatom or dinoflagellate food is needed for late copepodite and adult stages of *Acartia.*

Earlier observations of the feeding mechanisms of *Acartia* (Conover 1956; Gauld 1966), supplemented by recent cinematographic studies (Rosenberg 1980), revealed that the feeding mechanisms of *Acartia* are complex. Other observations suggest the possibility of chemosensory detection of food. For instance, Poulet and Marsot (1978) found that microcapsules enriched with homogenate of naturally occurring phytoplankton were ingested preferentially over nonenriched capsules by *A. clausi.* Lonsdale et al. (1979) found that predation rates by *A. tonsa* adults on nauplii of three other copepod species were significantly higher than cannibalism of conspecific nauplii. This suggests that *Acartia tonsa* adults can recognize conspecific nauplii, relative to those of other species.

The abundance of *Acartia* in food-rich inshore, particularly estuarine, environments may relate largely to its feeding ecology. Dagg (1977) found that *A. tonsa* needed fairly continuous food for survival and egg production. *Acartia tonsa* starved within 6-10 d with no or only intermediate additions of food, whereas other co-occurring copepod species survived for up to 20 d under constant starvation. Dagg concluded that *Acartia* is less well equipped than other copepod species to overcome periods of poor food conditions and subsequently exploit food-rich patches when they occur. However, in continuous food-rich conditions, such as estuaries, *Acartia* can outcompete other species due to its elevated fecundity.

CALANUS

It has long been known that species of the genus *Calanus* are omnivorous. Gut contents of North Atlantic *C. finmarchicus* contain remains of diatoms, dinoflagellates, silicoflagellates, *Phaeocystis,* coccolithophorids, radiolarians, tintinnids, molluscan larvae, and other crustaceans (Dakin 1908; Lebour 1922; Marshall 1924). Marshall (1924) found that the food remains in any single gut were mixed, that seasonal changes in gut contents reflected seasonal changes in the microplankton upon which the copepods fed, and that no particular preference was shown for any given species of phytoplankton. Guts of Pacific *C. tenuicornis, C. plumchrus,* and *C. cristatus* also contain diatom, coccolithophorid, silicoflagellate, tintinnid, and foraminiferan remains (Gienrikh 1958; Arashkevich 1969).

Numerous studies have shown that various species of *Calanus* eat a variety of cultured phytoplankton diets (Clarke and Gellis 1935; Fuller and Clarke 1936; Fuller 1937; Harvey 1937; Clarke and Bonnet 1939; Gauld 1951; Marshall and Orr 1952, 1955a, b, 1958, 1961; Conover 1960, 1966a, b, c; Mullin 1963; Anraku and Omori 1963; Anraku 1964a; Corner et al. 1967, 1972; Butler et al. 1969; Richman and Rogers 1969; Paffenhöfer and Strickland 1970; Paffenhöfer 1971, 1976a, b; Esaias and Curl 1972; Frost 1972, 1975, 1977; Gaudy 1974; Dagg 1977; Ikeda 1977; Schnack

1979, 1983; Vidal 1980a, b; Runge 1980; Gifford et al. 1981; Cox and Willason 1981; Huntley 1982). Other studies have examined the filter feeding of *Calanus* on natural particulate assemblages (Corner 1961; Cowey and Corner 1963; Adams and Steele 1966; Butler et al. 1970; McAllister 1970; Ikeda 1971; Taguchi and Ishii 1972; Gamble 1978; Cowles 1979; Hebert and Poulet 1980; Dagg et al. 1980, 1982; Boyd et al. 1980; Huntley 1981, 1982; Harris 1982). Additionally, *C. helgolandicus* and *C. pacificus* (possibly the same species) have been cultured on phytoplankton diets (Mullin and Brooks 1970a, b; Paffenhöfer 1970; Vidal 1980a, b).

Many concepts of copepod feeding that have risen to the status of paradigms are based upon experiments with *Calanus.* For instance, the concept that copepods preferentially select larger sized phytoplankton cells began as a result of Harvey's (1937) experiments with *C. finmarchicus.* Harvey fed the copepods on mixtures of large and small diatoms, and found that invariably more of the larger cells were eaten. Richman and Rogers (1969) reported that *C. helgolandicus* filtered significantly higher numbers of paired daughter cells (after cell division, but before final separation) of the diatom *Ditylum brightwelli,* than unpaired cells. Since the same species was offered, and the only difference was in terms of size rather than nutritional content, Richman and Rogers concluded that their results demonstrated size-selective feeding. Frost (1977) found that *C. pacificus,* presented with different-sized cells of the same diatom species, invariably ate large cells at a higher rate than small ones. Frost concluded that this differential filtration of cells of different sizes was purely mechanical and a function of variable retention efficiency of the intersetular distances of the filtering appendages (second maxillae) of the copepods. The results of Gamble (1978) support the notion of size-selective feeding on larger particles, in that *C. finmarchicus* mainly filtered the largest available cells, which were also the most abundant, during a spring diatom bloom in the North Sea. *Calanus* may also preferentially feed on chain-forming or spine-bearing diatoms because they occupy a larger volume and are more frequently encountered. Schnack (1979) fed *C. helgolandicus* on mixtures of chain-forming diatoms, and found that grazing was most intense upon species which had long spines. Gifford et al. (1981) obtained the same result using *C. finmarchicus.*

The results of some recent studies of *Calanus* feeding upon natural particulate assemblages often do not point to size-selective feeding. Cowles (1979) found that *C. chilensis* in the Peru upwelling were size-selective grazers at high food concentrations, but became less selective as total food concentration declined. Also, the size spectrum of particles ingested was much broader at low than at high food concentrations. Cowles concluded that while the mechanical sieve mechanism of filtering (Boyd 1976; Frost 1977) could explain the patterns recorded at high food concentrations, it could not explain the diet expansion at low food levels. Similarly, Harris (1982) found that *C. pacificus* grazed a broad size spectrum of phytoplankton, similar to that grazed by the much smaller copepod *Pseudocalanus.* Harris concluded that both species compete for the same food resource over a wide range of the particle-size spectrum. Hunger of animals also appears to influence size selection. Runge (1980) found differences in filtration rate versus cell size relations for starved versus well-fed *C. pacificus.*

The question of size-selective feeding by *Calanus* and other copepods is still unresolved. Inasmuch as laboratory studies using phytoplankton cultures as food allow reliable quantification of grazing on distinct size classes of food, they have the disadvantage of not offering copepods the broad size spectrum and nutritional array encountered in nature. Thus, because experimental conditions are partly artificial, patterns recorded may have questionable relevance to copepod behavior in nature. Feeding studies using natural particulate assemblages have the advantage of presenting animals with a food array found in nature. Unfortunately most such recent studies have quantified particle number and size by using electronic particle counters. Harbison and McAlister (1980) demonstrated numerous artifacts which can result from using electronic particle counters to quantify natural particle assemblages. They concluded that many reported patterns of copepod feeding resulting from such studies are not based upon experimental evidence.

The study of Huntley (1981) represents one of the few attempts to define copepod feeding upon natural particulate assemblages in which particle quantification was performed by visual rather than electronic means. Huntley found that three species of *Calanus* from the Labrador Sea exhibited no selective feeding on various phytoplankton species (>20 μm cell diameter) on the basis of size, shape, or species of cell. The copepods removed various phytoplankters in direct proportion to their abundance.

Another copepod feeding paradigm based on experiments with *Calanus* is that of the maximum ingestion rate plateau. Frost (1972) fed monospecific diatom cultures at different cell concentrations to adult female *C. pacificus* and found that the ingestion rate increased linearly with increasing food concentration up to a maximum rate, beyond which the ingestion rate remained constant with increasing levels of food. This maximum ingestion rate (saturation) was the same, in terms of carbon, for diatoms ranging in diameter from 11 to 87 μm, but as cell size increased the carbon concentration at which saturated feeding was achieved decreased. Frost (1972) concluded that *C. pacificus* can obtain their maximum daily ration at lower carbon concentrations when feeding on larger cells.

Conover (1978b) suggested that saturated feeding is likely an artifact of unnaturally high laboratory food concentrations, and concluded that food concentrations in nature are rarely, if ever, high enough to induce saturation. This view is supported by experiments of Reeve and Walter (1977) with *Acartia tonsa,* and Huntley (1981) with *Calanus.* Huntley found no evidence of a saturated ingestion rate for three *Calanus* species feeding on the spring diatom bloom in the Labrador Sea. Although Runge (1980) did record saturated feeding rates by *C. pacificus,* he found that there are seasonal changes in the level of food at which saturation is obtained.

Calanus also exhibits carnivorous feeding. Various species eat their own eggs (Conover 1960, 1966a), *Artemia* nauplii (Anraku and Omori 1963; Gaudy 1974), barnacle nauplii (Corner et al. 1974, 1976), and the nauplii of other species of copepods (Landry 1980, 1981). *Calanus finmarchicus* appeared to prefer phytoplankton over *Artemia* nauplii in the studies of Anraku and Omori (1963) and Gaudy (1974), but Landry (1981) found that *C. pacificus* can switch from eating diatoms to copepod nauplii, eating primarily whatever is most abundant.

Other food items eaten by *Calanus* include fecal pellets and other forms of detritus (Paffenhöfer and Strickland 1970). Paffenhöfer and Knowles (1979) reared *C. helgolandicus* from copepodite stage III to adult on a diet of fecal pellets alone. Boyd et al. (1980) found that *C. chilensis* in the Peru upwelling also appeared to utilize nonliving detrital particulates as a major component of its diet. Additionally, *C. helgolandicus* has been shown to eat "red mud" (microscopic particles of Fe_2O_3 residual from extraction of aluminum from bauxite), but the copepod does not

survive or feed well upon diatoms in the presence of "red mud" (Paffenhöfer 1972).

Although ingestion of nonnutritional particles such as "red mud" suggests that *Calanus* cannot discriminate between different food items, there is also limited evidence to suggest that a choice may occur. Huntley (1982) found that *C. pacificus* filtration rates on a large dinoflagellate during a red tide were minimal compared with those when a small diatom was used as food. He concluded that the persistence of the bloom may have been partly due to a lack of grazing, and that the dinoflagellate was likely avoided by the copepods.

Although some phytoplankton blooms may not be grazed because their component species are repulsive to copepods, other blooms may develop because of a lag in copepod feeding response. Cox and Willason (1981) found that production of the digestive enzyme laminarinase by *C. pacificus* requires presence of the substrate laminarin (the principal storage product of marine phytoplankton). Since there was at least a 1 d lag in the production of the enzyme in the copepods after addition of substrate, Cox and Willason proposed that such a time lag may be important in areas of bloom potential, since the lag would allow initial development of a bloom before it could be destroyed by grazing.

The role of *Calanus* and other copepods in cropping primary production has long been of interest (Harvey et al. 1935; Riley 1946; Cushing 1958, 1964; Cushing and Vucetic 1963; Dagg and Turner 1982) and, as expected, the impact of grazing has varied. Dagg et al. (1980) found that *C. chilensis* and two other large copepods consumed <5% of the daily carbon production in the Peru upwelling. Dagg et al. (1982) found that three large copepods (*Eucalanus bungii, Calanus* (*Neocalanus*) *cristatus* and *C.* (*N.*) *plumchrus*) removed 6-25% of the daily primary production during the spring bloom in the Bering Sea. Dagg and Turner (1982) found that during the spring bloom in the New York Bight and Georges Bank areas a copepod community dominated by *C. finmarchicus* and *Pseudocalanus* grazed 15-48% of the daily primary production. In both areas, grazing impact was highest on the outer shelf (30-48% of primary production) because of large populations of *C. finmarchicus.* In other regions, grazing appears particularly important. Frost (1980) stated that the lack of seasonal variation in the phytoplankton biomass of the subarctic North Pacific, where phytoplankton apparently never reach bloom concentrations even though conditions favorable to blooming do occur, is largely due to continuous grazing by subadults of *C.* (*N.*) *plumchrus* and *C.* (*N.*) *cristatus.* Since adults of these species do not feed, reproduction is not dependent upon phytoplankton pulses, and large numbers of juvenile copepods are present in the epipelagic waters during the season when phytoplankton blooms should occur.

Frost et al. (1983) confirmed that *Calanus* (*Neocalanus*) *cristatus* and *C.* (*N.*) *plumchrus* CV copepodites could feed on the low concentrations of small phytoplankton cells found in the subarctic Pacific. In addition, these copepodites exhibited predatory feeding upon copepodites of the small copepod *Oithona similis.*

In conclusion, it appears that species of *Calanus* are omnivorous, in that they are capable of carnivorous as well as herbivorous feeding. However, it is likely that this genus is primarily and broadly herbivorous, resorting to carnivory mainly during periods of phytoplankton paucity (Corner et al. 1974; Digby 1954).

CENTROPAGES

Members of the genus *Centropages* are broadly omnivorous. Gut contents have included remains of diatoms, dinoflagellates, coccolithophorids, tintinnids, copepods, and molluscan larvae (Lebour 1922; Marshall 1924, 1949; Marshall and Orr 1966). Cultured phytoplankton diets have been fed to *C. hamatus* (Kiørboe et al. 1982; Marshall and Orr 1966; Gauld 1951; Gauld and Raymont 1953; Smith and Hall 1980; Klein Breteler 1980), *C. typicus* (Cowles and Strickler 1983; Gaudy 1974; Dagg 1977, 1978; Tomasini and Mazza 1978; Smith and Hall 1980), and *C. furcatus* (in the Atlantic = *C. velificatus* — see Fleminger and Hulsemann, 1973) (Paffenhöfer and Knowles 1980). *Centropages* is also capable of carnivorous feeding (Anraku and Omori 1963; Gaudy 1974; Paffenhöfer and Knowles 1980; Conley 1983).

There is a lack of consensus on the relative importance of plant and animal food in *Centropages* diets. Anraku and Omori (1963) examined the feeding responses of *C. hamatus* and *C. typicus* on diets of *Artemia* nauplii and diatoms, either singly or in combination. Both species of *Centropages* ate both types of food, but animal food (*Artemia*) was preferred. However, Gaudy (1974) found that *C. typicus* fed equally well on *Artemia* nauplii and phytoplankton cultures. Paffenhöfer and Knowles (1980) found that the subtropical species, *C. velificatus,* ingested a higher percentage of its body nitrogen as copepod nauplii (laboratory-reared *Pseudodiaptomus coronatus*) than as unialgal phytoplankton (*Rhizosolenia*). Conversely, Conley (1983) found that the temperate species, *C. hamatus,* ingested a higher proportion of its body carbon as natural estuarine phytoplankton (predominantly small flagellates) than as cooccurring wild copepod nauplii (primarily *Acartia hudsonica* or *A. tonsa*). Such differences may reflect the use of different food sources, different experimental procedures and methods of measurement, or possibly real differences between subtropical continental shelf *(C. velificatus)* and temperate estuarine (*C. hamatus*) species.

There have been few investigations of the grazing of *Centropages* on natural particulate matter. Dagg and Grill (1980) found that ingestion rates of *C. typicus* in the New York Bight were usually less than maximal, and concluded that ingestion rates were closely related to food quality because of the narrow range of available food concentrations. Dagg et al. (1980) calculated that in the Peru upwelling the population of *Centropages brachiatus* consumed an average of 1.5 $\mu gC/m^2$ per d. Since average primary production rates were >1 gC/m^2 per d, Dagg et al. calculated that the grazing stress of *C. brachiatus* and two other large copepods (*Eucalanus inermis* and *Calanus chilensis*) was always < 5% of the daily carbon production. Cowles (1979) examined the feeding responses of the same three species of copepods in the Peru upwelling. He found that *C. brachiatus* was a size-selective grazer at high food concentration, and exhibited decreased selectivity as total food level declined.

Boyd et al. (1980) found that in the Peru upwelling *C. brachiatus* migrated into the food-rich upper 5 m at night, but did not show a migration pattern when food was scarce. Using gut fluorescence techniques, Boyd et al. found no indication that *C. brachiatus* was grazing phytoplankton in proportion to its abundance, and concluded that this reflected predatory feeding in addition to grazing.

As with *Acartia tonsa,* Dagg (1977) found that *C. typicus* is intolerant of starvation and intermittent food. He concluded that *C. typicus* is therefore sensitive to small-scale patchiness. The migration data of Boyd et al. (1980) support this proposal, in that *C. brachiatus* actively moved into food-rich waters. Their data also support other observations suggesting that carnivory is a major component of *Centropages* ecology.

PARACALANUS

Limited available literature suggests that small (< 1 mm adult body length) copepods of the genus *Paracalanus* are primarily herbivorous. Lebour (1922) found diatom and coccolithophorid remains in the guts of *P. parvus,* and several *Paracalanus* species have been fed phytoplankton cultures or natural particulate assemblages (Marshall and Orr 1966; Ikeda 1977; Checkley 1980; Bartram 1981; Price et al. 1983). Bartram (1981) showed that *P. parvus* was more efficient at capturing small particles than was *Acartia,* and that *P. parvus* fed at a higher rate on small particles. Sorokin et al. (1970) stated that *P. parvus* can also filter bacteria.

The calculations of Paffenhöfer (1982) indicate that *Paracalanus* can have a substantial grazing impact on natural systems. Applying his own grazing rates for *Paracalanus* sp. from the southeastern shelf of the United States to the numbers of *Paracalanus denudatus* reported by Dagg et al. (1980) in the Peru upwelling, Paffenhöfer calculated that *Paracalanus* could graze an average of 33% of the primary production in the Peru upwelling.

PSEUDOCALANUS

Corkett and McLaren (1978:54-80) reviewed feeding studies published prior to 1977, which showed that *Pseudocalanus* is mainly a filter feeder, ingesting a variety of diatom, coccolithophorid, flagellate, and radiolarian foods. However, Marshall (1949) found crustacean remains in *Pseudocalanus* guts, and Corkett and McLaren (1978) stated that females will cannibalize their own nauplii. *Pseudocalanus* also ingests detrital particles (Poulet 1976). Nonetheless, Corkett and McLaren concluded that *Pseudocalanus* is overwhelmingly herbivorous. This conclusion is supported by culture studies of Paffenhöfer and Harris (1976) and Vidal (1980a). In both cases, *Pseudocalanus* was cultured from fertilized eggs to adults on diatom diets.

Recent studies of grazing on natural particulate assemblages (Poulet 1978; Koeller et al. 1979; Harris 1982) reveal that *Pseudocalanus* ingests a broad spectrum of particle sizes. Poulet (1973, 1974, 1978) reported seasonal shifts of grazing on the most abundant particles, regardless of size, and concluded that *Pseudocalanus* is an unselective opportunistic grazer. Harris (1982) found that *Pseudocalanus* grazed a size spectrum of phytoplankton similar to that grazed by *Calanus,* which is 10 times larger in terms of body weight.

Dagg (1977) found that *Pseudocalanus* can withstand starvation for at least 16 d, and can produce eggs under discontinous starvation at rates equivalent to those for continuously fed animals. Dagg concluded that *Pseudocalanus* can metabolically remove itself from poor food conditions and wait for food-rich patches. Vidal (1980a) demonstrated that the growth rate of *Pseudocalanus* is relatively insensitive to food concentration. Vidal concluded that this contributes to survival fitness of *Pseudocalanus* in adverse conditions which frequently occur in its temperate and boreal habitat.

TEMORA

Early gut content studies (Lebour 1922; Marshall 1949) revealed that *Temora* is omnivorous, eating diatoms, dinoflagellates, the haptophycean *Phaeocystis,* radiolarians, and other crustaceans. Gauld (1966) stated that *Temora* is a filter feeder that also feeds as a grasping predator.

Numerous studies show that the temperate species *Temora longicornis* eats a variety of cultured phytoplankton diets (Gauld 1951, 1953; Gauld and Raymont 1953; Raymont 1959; Conover 1959; Marshall and Orr 1966; Berner 1962; Harris and Paffenhöfer 1976a; Cushing 1958; Smith and Hall 1980; Schnack 1983; Weiss 1983). Studies reaching similar conclusions for the subtropical/tropical species *T. turbinata* and *T. stylifera* include those of Gaudy (1974), Ikeda (1977), and Paffenhöfer and Knowles (1978, 1980). *Temora longicornis* has also been cultured from fertilized egg to adult on various flagellate or diatom diets (Corkett 1967, 1970; Corkett and Zillioux 1975; Harris and Paffenhöfer 1976a; Klein Breteler 1980).

Studies of grazing of *Temora* on natural particulate assemblages have had inconsistent results. Hargrave and Geen (1970) found that *T. longicornis* ate all sizes of flagellates present in natural estuarine water, and that feeding rates were highest on larger cells, even though smaller cells were most abundant. They also reported that *T. longicornis* did not eat chain-forming diatoms of the genus *Chaetoceros,* or other chain-formers, even though these were the numerically dominant phytoplankters. This seems peculiar, since Harris and Paffenhöfer (1976a) have cultured the same copepod on unialgal diets of chain-forming diatoms, and Gaudy (1974) and Paffenhöfer and Knowles (1978) demonstrated that *T. stylifera* and/or *T. turbinata* ate a variety of chain-forming diatoms.

Poulet (1978) and Mayzaud and Poulet (1978) reported that *T. longicornis* feeding on natural particles was an opportunistic grazer, and nonselective with regard to particle size. Mayzaud and Poulet (1978) also found that ingestion rate was linear with increasing food concentration, regardless of particle size. In a similar study with *T. longicornis* feeding on natural particles, O'Connors et al. (1980) found that different ingestion rate versus food concentration relations emerged when the food particle assemblage had differences in species composition and size distribution. Maximum ingestion rates were higher when *T. longicornis* fed upon larger sized chain-forming diatoms than on naked microflagellates.

Temora is also capable of carnivorous feeding. Various species eat corpses of other copepods (Lowndes 1935), their own eggs (Gaudy 1974), *Artemia* nauplii (Gaudy 1974), and the nauplii of other copepods (Paffenhöfer and Knowles 1980). Although Gaudy (1974) found that *T. stylifera* had a higher food intake when feeding on *Artemia* nauplii than when feeding on various phytoplankton cultures, Paffenhöfer and Knowles (1980) found that *T. stylifera* ingested more food as phytoplankton than as nauplii of another copepod.

In addition to phytoplankton and zooplankton foods, *T. longicornis* has ingested oil particles following a tanker wreck, with no apparent ill effect (Conover 1971). Also, Paffenhöfer and Knowles (1979) found that *T. stylifera* ate fecal pellets of the nauplii of another copepod at about the same rate as it ate large phytoplankton cells (*Rhizosolenia*) having cell volumes comparable with those of small fecal pellets.

CYCLOPOID COPEPODS

Oithona

There is limited information on the feeding habits of several species of *Oithona,* and much of it is contradictory. Taken as a whole, however, members of the genus apparently are omnivorous.

Lebour (1922) concluded that *O. similis* is primarily herbivorous after finding diatom remains in its gut. Murphy (1923) cultured *O. nana* on pieces of ground kelp, although she stated that the guts of field-caught specimens contained diatom and copepod remains. Gauld (1966) and Marshall and Orr (1966) stated that *O. similis* feeds little on phytoplankton, and then only on large cells. Since Gauld (1966) and Marshall and Orr (1966) found that *O. similis* eats the nauplii of other copepod species, they concluded that the species is primarily carnivorous. Timonin (1969, 1971) reached the same conclusion for several other species of *Oithona.* However, Petipa et al. (1970) considered *Oithona* copepodites to be omnivorous and only adults to be exclusively carnivorous.

Oithona nana can eat either *Acartia* or *Calanus* nauplii (Lampitt 1978; Lampitt and Gamble 1982), but it can also ingest unialgal cultures of five phytoplankton species ranging in size from 2.7 to 67.0 μm in diameter (Lampitt and Gamble 1982). Likewise, Hargrave and Geen (1970) and Poulet (1978) found that *O. similis* fed upon natural particulate assemblages and ingested various phytoplankton species, but Poulet suggested that *O. similis* may be an inefficient grazer. This may partly explain why Dagg and Turner (1982) calculated that a copepod community dominated by *O. similis* was grazing > 100% of the primary production/day in continental shelf waters. Nonetheless, diets consisting solely of phytoplankton cultures have been used to rear *O. nana* (Haq 1965) and *O. colcarva* (Lonsdale 1981).

Corycaeus

Little is known of the feeding habits of *Corycaeus.* Lebour (1922) found remains of diatoms, dinoflagellates, and coccolithophorids in *C. anglicus* guts, and she classified this species as primarily herbivorous. Wickstead's (1962) examination of preserved Indo-Pacific species of *Corycaeus* led him to conclude that they were mainly carnivorous. Timonin (1969, 1971) also classified the genus as carnivorous. Indeed, Gophen and Harris (1981) found that *C. anglicus* ate *Artemia* nauplii, and Johnson (1969 — cited in Gibson and Grice 1978) classified this species as a raptorial carnivore with *Acartia* spp. as primary prey. Nonetheless, Landry and Zakar (unpubl. data — cited in Landry 1981) found that stomachs of *C. anglicus* may be full of phytoplankton during bloom conditions.

Oncaea

The feeding habits of all species of the genus *Oncaea* are largely a matter of conjecture. Gienrikh (1958) mentioned that *O. conifera* guts contain coccoliths and remains of pennate diatoms, but Wickstead (1962) classified the genus as carnivorous. Bernard (1963a) and Wickstead (unpubl. data) (both cited by Marshall 1973) hypothesized that *Oncaea* is actually a temporary plankter, and that it either feeds in bottom sediments (Bernard) or attaches to, and feeds upon, gelatinous zooplankton (Wickstead). While there are little data to support the hypothesis that *Oncaea* is not truly holoplanktonic, Alldredge (1972) found that *Oncaea mediterranea* can feed upon abandoned appendicularian houses and the microplankton attached to them.

PLANKTONIC HARPACTICOID COPEPODS

Many species of harpacticoids inhabit epibenthic or meiobenthic habitats, and it is likely that benthic harpacticoids are a major portion of the "unidentified harpacticoid" component of the diets of demersal larvae of many fishes. Some benthic harpacticoids have been cultured (Omori 1973; Walker 1981) on a variety of phytoplankton diets. In addition, feeding studies reveal that certain species ingest phytoplankton, protozoans, detritus (Harris 1977; Heinle et al. 1977; Brown and Sibert 1977; Rieper and Flotow 1981), and bacteria (Rieper 1978, 1982; Brown and Sibert 1977).

Information on the feeding habits of planktonic harpacticoids is sparse. Lebour (1922) found phytoplankton and copepod remains in the guts of *Euterpina acutifrons.* This species has also been cultured on a variety of unialgal or mixed phytoplankton cultures (Bernard 1963b — cited in Omori 1973; Haq 1972; Nassogne 1970; Neunes and Pongolini 1965; Zurlini et al. 1978). The only information located on feeding by *Microsetella* is that *M. rosea* guts contain coccoliths, green remains, and radiolarian spines (Gienrikh 1958). Bjornberg (1965) found that *Macrosetella gracilis* requires the blue-green alga *Trichodesmium* as a substrate. Roman (1978) confirmed this, and found that *M. gracilis* ingested *Trichodesmium* at rates equivalent to 90-126% of its body weight/day.

COPEPOD NAUPLII

All copepods, regardless of adult body size, begin life as small nauplii. Copepods molt through six progressively larger naupliar stages, followed by six copepodite stages, the sixth being the adult. Although subadult copepods usually outnumber adults by orders of magnitude in most marine waters (for example, compare numbers in Turner 1982), the feeding habits of these juveniles, particularly nauplii, are poorly known. Intuitively one might expect that copepod nauplii eat smaller phytoplankton cells than adults, but this is not always the case.

Marshall and Orr (1956) fed *Calanus finmarchicus* nauplii on cultures of small flagellates, coccolithophorids, chain-forming diatoms, and dinoflagellates. Smaller naupliar stages usually did not eat smaller sized cells than did larger naupliar stages. Rather, some stages of nauplii ate the same types and sizes of food as adults. Marshall and Orr found that naupliar stages I and II did not feed, presumably because their anus had not yet formed. From naupliar stage III onward, cells of up to 20 μm in diameter were eaten, but flagellates as small as 2-4 μm in diameter were not eaten.

Nauplii of other copepod species do not always exhibit these same patterns. Mullin and Brooks (1967) found that *Rhincalanus nasutus* nauplii could not eat some species of large diatoms which were eaten by adults. Mullin and Brooks (1970a) fed unialgal cultures of *Ditylum brightwelli* (a large diatom) and *Thalassiosira fluviatilis* (a small diatom) to nauplii of *R. nasutus* and *Calanus helgolandicus. Calanus* nauplii were unable to eat the large diatom, but grew well when eating the small one. The reverse was true for *Rhincalanus* nauplii, which are larger than those of *Calanus.* Apparently *Rhincalanus* nauplii are large enough to capture and ingest the large diatom, but their filtering appendages are too coarse to collect the small diatom. The success of naupliar feeding is apparently important to the ultimate success of a copepod. Mullin and Brooks (1970b) found that the body weights of late-stage copepodites and growth efficiencies were functions of food concentrations encountered by copepods as nauplii.

Nauplii of *Calanus helgolandicus* have been cultured on diets of several dinoflagellate and chain-forming diatom species (Paffenhöfer 1970, 1971, 1976a). Ingestion rates increased with both increasing food concentration and particle size. Unialgal diets of chain-forming diatoms also have been used to rear nauplii of

Pseudocalanus elongatus and *Temora longicornis* (Paffenhöfer and Harris 1976; Harris and Paffenhöfer 1976a, b).

Allan et al. (1977) examined the feeding of naupliar stages III-VI of three estuarine copepods (*Eurytemora affinis, Acartia tonsa,* and *A. clausi*) on natural particulates. In a few cases there was evidence of size-selective feeding, but most feeding was unselective.

Paffenhöfer and Knowles (1978) offered nauplii of *Eucalanus pileatus, Temora stylifera,* and *T. turbinata* mixtures of two chain-forming and one large solitary (*Rhizosolenia*) diatom species. *Eucalanus pileatus* nauplii larger than stage IV, copepodites, and adults ingested similar percentages of the three phytoplankters. However, the nauplii of the two *Temora* species ingested only one of the chain-formers (*Skeletonema costatum*), and only nauplii larger than stage IV ingested the other *(Leptocylindrus danicus).* Ingestion of *Rhizosolenia* by *Temora* subadults did not commence until copepodite stage II. Paffenhöfer and Knowles (1978) concluded that the size range of cells eaten by *Temora* nauplii was 4-20 μm diameter, whereas that for *Eucalanus* nauplii was 4.5 to > 100 μm.

Fernandez (1979a, b) fed *Calanus pacificus* nauplii on mixtures of cultured phytoplankton and artificial foods such as plastic beads, pollen grains, or detritus from senescent algal cultures. Phytoplankton were selected over artificial foods, but phytoplankton cells > 45 μm or < 11 μm in longest dimension were not eaten well, due to the inability of nauplii to manipulate larger cells or to retain smaller ones. Fernandez found that ingestion rates were dependent upon algal size. Further, dinoflagellates, regardless of size, were ingested at lower rates than diatoms.

In conclusion, most copepod nauplii appear to eat primarily phytoplankton, the size and type of which varies with copepod species and stage of nauplius. Thus far, however, the feeding habits of nauplii of only about a dozen copepod species have been examined. Considering the high numbers of nauplii usually present in the sea, the current lack of information on the dynamics of feeding by copepod nauplii precludes realistic understanding of pelagic ecosystem dynamics.

TINTINNIDS

Tintinnids are ciliate protozoans which appear to be primarily herbivorous. Lebour (1922) found that *Cittarocyclis serrata* ate eight species of dinoflagellates, one species of diatom, and two species of tintinnids. Since the tintinnids and dinoflagellates were present only in summer, and dinoflagellates were the main food items of the tintinnids, Lebour classified *C. serrata* as a "peridinian feeder."

Stoecker et al. (1981) also found dinoflagellates to be important in the diet of *Favella ehrenberghii.* Successful culture of this tintinnid required dinoflagellate food. Further, in selective feeding experiments, dinoflagellates (11 species) were always consumed, but there was little if any grazing of nondinoflagellates (12 species of diatoms, microflagellates, and chlorophytes). Selection of dinoflagellates was not on the basis of size alone. One dinoflagellate, *Amphidinium carterae* was not eaten; this species has been suggested to produce ectocrines which repel grazers. Blackbourn (1974), however, found that *A. carterae,* as well as many nondinoflagellates were eaten by various tintinnid species (see table 2 of Rassoulzadegan and Etienne 1981 for a summary of Blackbourn's unpublished work). Stoecker et al. (1981) concluded that *F. ehrenberghii* is a specialized dinoflagellate predator which consumes few, if any, of the nondinoflagellates tested.

While the conclusion of Stoecker et al. (1981) may apply to *F. ehrenbergii,* it clearly does not apply for some other tintinnids. Gold (1968, 1969a, b, 1970, 1971, 1973) has cultured five other species of tintinnids on diets of microflagellates. Only one of the five tintinnids required dinoflagellate food for successful culture.

Heinbokel (1978a) also found that five additional tintinnid species ingested three species of microflagellates and one species of coccolithophorid, either singly or in combination. For the three tintinnid species studied most extensively, one showed increasing ingestion rates with increasing food concentration, with no plateau. The other two species exhibited increasing ingestion rates with increasing food up to a saturation plateau. Since these tintinnids ingested 10-20% of their body weight per day, converted this ration to tintinnid biomass with > 50% efficiency, and exhibited doubling times of 12-24 h, Heinbokel (1978a) and Heinbokel and Beers (1979) concluded that tintinnids are capable of substantial grazing impact on nanoplankton. Capriulo and Carpenter (1983) similarly concluded that the tintinnid populations of Long Island Sound were responsible for ingesting 27% of the annual primary productivity in the estuary. This community ingestion was equivalent to that calculated for the Long Island Sound copepod population.

Rassoulzadegan and Etienne (1981) examined the feeding of *Stenosemella ventricosa* on natural particulates, and reported this tintinnid to feed on nanoplankton-sized particles (< 27 μm in diameter) primarily in the 3-12 μm size range. Ingestion rate was a linear function of food concentration, with no saturation over the range of food concentrations examined. The tintinnid ingested about 66% of its body weight per day. After feeding for a time on a certain size range of particles, it adjusted its grazing pressure to other size categories which had not been previously grazed.

Thus it appears that various species of tintinnids feed mainly on nanoplankton-sized flagellates and/or dinoflagellates. Part of the lack of agreement on tintinnid diets probably is due to the large variation in size of lorica oral diameters of various tintinnid species. For instance, the oral lorica diameter of *Eutintinnus pectinis* is 20 μm (Turner and Anderson 1983), whereas that of *Favella panamensis* is > 100 μm (Turner unpubl. obs.). These differences are important since various tintinnid species have been shown to ingest particles only < 41-45% of their lorica oral diameter (Spittler 1973; Heinbokel 1978b). In addition, other phytoplankters such as the flagellate *Olisthodiscus luteus* appear to be unsuitable as food for some tintinnids for reasons related to toxicity rather than size (Verity and Stoecker 1982).

There has been abundant speculation that tintinnids are a major trophic link between the nanoplankton upon which they feed, and larger plankters such as copepods and larval fish which might prey upon tintinnids (Beers and Stewart 1967; Heinbokel and Beers 1979; Pomeroy 1974; Parsons and Takahashi 1973). Apparently the first synoptic demonstration of this is the observation of Turner and Anderson (1983) that *Eutintinnus pectinis* cells containing the microflagellate *Chroomonas amphioxea* were ingested by the copepod *Acartia hudsonica.*

APPENDICULARIANS

Appendicularians are gelatinous tunicates which are ubiquitous throughout the ocean. They feed by a ciliary mucoid mechanism using an external mucus filter. A spherical mucus "house" expands around the animal, through which water is pumped by action of the animal's tail, and particles are trapped on incurrent filters. When the "house" becomes clogged, the animal discards it

and secretes a new one (Alldredge 1977; Alldredge and Madin 1982).

Appendicularians feed primarily on nanoplankton-sized particles (Alldredge 1977, 1981). They can retain particles as small as 0.1 μm in diameter, and particles < 2 μm are the largest component of their gut contents (Alldredge and Madin 1982). Paffenhöfer (1973, 1976c) has cultured *Oikopleura dioica* and *Frittilaria borealis* for multiple generations on diets of the microflagellates *Isochrysis galbana* and *Monochrysis lutheri,* and the small diatom *Thalassiosira pseudonana. Oikopleura dioica* also exhibits substantial grazing on bacterioplankton (King 1982; King et al. 1980).

Alldredge (1981) measured in situ filtration rates of two appendicularian species and found that, compared with filtration rates of other zooplankters, those of appendicularians were high. Multiplying these rates by the number of animals present, Alldredge found that appendicularians could filter clear up to 38% of each cubic meter per day, a rate which exceeded particle replacement by phytoplankton growth.

Appendicularian growth rates are high, and populations of these animals can "explode" in response to bacterioplankton and nanophytoplankton blooms (King 1982; Paffenhöfer 1976c; Alldredge and Madin 1982). Since appendicularians feed on nanoplankton-sized particles, and are directly consumed by larval fish (Shelbourne 1953, 1957, 1962; Uotani et al. 1981; Wyatt 1974), they provide a major trophic link between the lower and upper parts of the pelagic food chain.

MARINE CLADOCERANS

Although most cladoceran species live in freshwater, three genera (*Podon, Evadne,* and *Penilia*) comprising seven species inhabit the sea. Due to parthenogenic reproduction, cladoceran populations can "explode" under favorable conditions and may become numerically dominant zooplankters at a given place and time (Della Croce and Venugopal 1973; Gieskes 1971; Onbe 1977).

The existing literature on the feeding habits of marine cladocerans is sparse and somewhat contradictory. For instance, Conover (1978a: 272-273) stated that "*Evadne* and *Podon* seem to feed largely on discrete particles and perhaps detritus...but no experimental observations have been made." Examination of feeding appendages prompted Nival and Ravera (1979) to suggest that *Evadne spinifera* possesses the ability to catch and hold animal prey or large algal cells, although no confirming observations were reported. Lebour (1922) found green remains of *Phaeocystis* in the guts of *Evadne normanni* and soft brown remains with no apparent structure in the guts of *Podon intermedius.* Bainbridge (1958) also reported unrecognizable remains in the guts of *E. normanni.* Pavlova (1967) found no phytoplankton remains in the guts of *E. spinifera* and *E. tergestina.* Since some of the particles were "very much like chitin," Pavlova concluded that *Evadne* eats zooplankton and detritus. White (1980) observed that the gut contents of *E. normanni* collected during a bloom of the red tide dinoflagellate *Gonyaulax excavata* contained "yellow-brown material consisting of chromatophore-like bodies" which he assumed to be remains of *G. excavata.* The cladocerans also contained intact cells of the large (up to 300 μm diameter) diatom *Coscinodiscus asteromphalus.*

The only other marine cladoceran that has received any study is *Penilia avirostris,* which Pavlova (1959) stated is an indiscriminant filter feeder utilizing only particles < 8 μm in diameter. Gore (1980) reported, however, that this species ingested glass beads of up to 50 μm in diameter but preferred beads < 20 μm. Several Soviet investigators have stated that *P. avirostris* feeds on small phytoplankton and detritus, but primarily on bacteria (Pavlova 1959; Pavlova and Sorokin 1970 — cited in Conover 1978a; Sorokin et al. 1970; Pavlova et al. 1973; Sorokin 1973, 1981; Petipa et al. 1973). Nonetheless, since copepods as large as *Rhincalanus cornutus* (body length = 2.7 mm for males, 3.6 mm for females), *Eucalanus attenuatus* (body length = 3 mm for males, 4-5 mm for females), and *Clausocalanus mastigophorus* (body length = 1.0-1.5 mm for males, 1.2-1.8 mm for females) (lengths from Rose 1933 and Frost and Fleminger 1968) also have been stated to ingest 10-75% of their body carbon per day as bacteria (Sorokin 1981), the claims that cladocerans eat primarily bacteria appear deserving of further investigation.

In summary, there is disagreement about, or extreme variability in, the nature and sizes of food eaten by marine cladocerans. The paucity of knowledge on the feeding habits of these animals is reflected by the fact that in his 278-page review of feeding by marine animals, Conover (1978a) devoted nine sentences (p. 272, 273, 293, 294) to summarizing existing knowledge on marine cladoceran feeding.

BARNACLE NAUPLII

Barnacle nauplii appear primarily herbivorous. Lebour (1922) found that guts of several species contained remains of green flagellates, diatoms, and *Phaeocystis.* Moyse (1963) compared the suitability as food of unialgal cultures of 17 species of microflagellates, dinoflagellates, and diatoms for nauplii of 5 barnacle species. The palatability of various phytoplankters to nauplii of different barnacles varied. Two dinoflagellates, *Amphidinium* and *Prymesium,* were unsuitable food for all nauplii, and *Chlorella* and *Dunaliella,* while eaten, did not allow nauplii to develop completely. *Balanus* nauplii could be reared on diatoms but not on flagellates; for *Chthamalus* nauplii the reverse was true. *Eliminius* nauplii grew well on a wide range of phytoplankters. Nauplii of the oceanic barnacle *Lepas* grew well on diets of flagellates but not on diets of diatoms. Moyse (1963) suggested that growth was better because flagellates are usually more abundant than diatoms in oceanic waters. Conversely, nauplii of the arctic/boreal barnacle *Verruca* grew best on diatoms, which usually dominate the phytoplankton in arctic/boreal waters. Moyse suggested that the unsuitability of chain-forming diatoms as food for nauplii of some species was due to their clogging the finely setulated filtering appendages of the nauplii. Clogging did not occur when these species fed upon small flagellates. Moyse concluded that nauplii of different barnacle species have different diet requirements.

Other species of barnacles have been reared successfully through naupliar stages on unialgal or mixed diets of diatoms and microflagellates (Wisely 1960; Moyse 1960; Barnes and Costlow 1961; Tighe-Ford et al. 1970; Karande 1974a, b). Further, Costlow and Bookout (1957, 1958) reared two other barnacle species on diets of *Chlamydomonas,* but found that completion of development required addition of starfish *(Arbacia)* eggs in the later stages of development. Aside from the observations of Costlow and Bookout, however, it appears that most barnacle nauplii are primarily herbivorous although the types of phytoplankton eaten vary with barnacle species.

GASTROPOD LARVAE

Most gastropod larvae examined feed on phytoplankton. Gut contents contained remains of a variety of diatoms (Lebour 1922),

and Thompson (1959) fed the diatom *Phaeodactylum tricornutum* to larvae of numerous gastropod species.

Fretter and Montgomery (1968) examined the feeding of veligers of 19 gastropod species on cultures of 3 dinoflagellate, 7 microflagellate, 4 nanochlorophyte, and 4 diatom species. Some phytoplankters clearly were unsuitable food. The flagellate *Olisthodiscus* was either undigested or, for some veligers, was toxic. *Monochrysis* was also lethal to veligers of four species. However, most of the phytoplankters were readily ingested, except for large (> 30 μm cell diameter) or chain-forming species, which clogged the preoral cilia of some veligers.

Mapstone (1970) fed unialgal cultures of the dinoflagellate *Exuviaella baltica* and two microflagellates to veligers of *Nassarius reticulatus* and *Crepidula fornicata.* Based on activity of veligers while feeding, the microflagellates were good food for *N. reticulatus* veligers but *E. baltica* was not. The reverse was true for *C. fornicata* veligers. Pilkington and Fretter (1970), using the same phytoplankters as food, examined growth of veligers of the same species and reached the same conclusions. Of five additional microflagellate species, four were poor foods, and of these two were toxic. A diatom was also poor food because the frustules were too large for convenient ingestion, and they appeared to stimulate gut pulsations, which Pilkington and Fretter considered indicative of irritation. Pilkington and Fretter also found that veligers of both gastropods ingested several strains of bacteria.

The limited available information suggests that gastropod larvae are primarily phytoplankton, and possible bacterioplankton, feeders.

LIMACINA

Limacina is a genus of pteropod (holoplanktonic molluscs). Although gymnosomatous or nonshelled pteropods appear to prey principally, or exclusively, upon thecosomatous or shell-bearing pteropods (Lalli 1970, 1972; Conover and Lalli 1972, 1974), thecosomes are ciliary-mucoid filter feeders (Yonge 1926; Morton 1954; Lalli 1970; Gilmer 1972, 1974; Silver and Bruland 1981). The guts of *Limacina retroversa,* a thecosome, contained remains of diatoms (Lebour 1922) and Morton (1954) assumed that it ate dinoflagellates and nanoplankton as well. Paranjape (1968) found that *L. helicina* guts contained some remains of chain-forming diatoms, but that remains of dinoflagellates and tintinnids were most abundant.

These limited observations suggest that species of *Limacina* are primarily herbivorous filter feeders.

DISCUSSION

Several points should emerge from this review: 1) Most zooplankters, particularly copepods, appear to be omnivorous feeders; 2) we still have too little information on the exact mechanisms by which many zooplankters capture and select (or even if some select) various types of food; and 3) we know next to nothing about the feeding habits in nature of some very abundant zooplankters.

Since the time of Lebour (1922) it has been known that most copepods are omnivorous, ingesting plant, animal, and detrital foods. In the absence of detailed examinations of gut contents and quantitative comparisons of ingestion of various types of food, attempts to use mouthpart structures to classify copepods as herbivores or carnivores (Itoh 1970; Arashkevich 1969) appear unwarranted. Indeed, some copepods thought to be primarily carnivorous (pontellids) have been shown to ingest a variety of phytoplankters (Turner 1978; Conley 1983) and some "typical" herbivores such as *Calanus* have been shown to feed as carnivores (Corner et al. 1974, 1976; Landry 1980, 1981). Missing for most species are not only qualitative descriptions of food items ingested in nature, but also quantitative comparisons using natural food of the relative importance of herbivorous and carnivorous feeding. The studies of Paffenhöfer and Knowles (1980), Landry (1981), and Conley (1983) represent steps in that direction. Observations by Landry (1981) that *Calanus* can switch from eating phytoplankton to eating zooplankton, and vice versa, suggest that copepod feeding preferences are quite plastic. If this pattern is generally applicable, the idea that alteration of phytoplankton species assemblages may result in adverse trophodynamic alteration of zooplankton and ichthyoplankton assemblages appears simplistic. The true pattern may be that most zooplankters, including larval fish, eat their "favorite" food if it is present and abundant, and if not, they make do by eating something else.

Many classic concepts of the manner by which copepods gather food have recently been shown to require revision. The "textbook" description of copepods using bristled appendages such as the second maxillae as open rakes to strain particles from water by filtration (Esterly 1916; Cannon 1928; Lowndes 1935; Marshall and Orr 1955c; Gauld 1966; Boyd 1976; Nival and Nival 1976; Frost 1977) has been altered by cinematographic studies which show that these appendages behave as solid paddles, capturing whole parcels of water containing food particles which are brought to the mouth with hardly touching setae or setules (Alcaraz et al. 1980; Koehl and Strickler 1981; Paffenhöfer et al. 1982; Strickler 1982). There also is increasing evidence that "selection" of various types of food, or even induction of feeding, has a chemosensory component (Poulet and Marsot 1978, 1980; Friedman and Strickler 1975; Cox and Willason 1981). Although food particle size may broadly dictate what types of food items can be physically handled by the feeding apparatus of a zooplankter, and although certain sizes of food items appear to be more efficiently ingested than others, it is becoming clear that selective feeding, if and when it occurs, is not solely on the basis of particle size. Indeed, recent experimental (Harris 1982; Huntley 1981) and gut content (Hayward 1980) studies have revealed that different sized copepods compete for the same broad size array of food items. In view of these observations, and those of Harbison and McAlister (1980) on artifacts associated with the use of electronic particle counters to study selective feeding by zooplankters upon natural particulate assemblages, it may be that we need to "unlearn" some of what we presently "know" of zooplankton feeding patterns.

The largest problem with the present state of knowledge of zooplankton feeding is that we have very little information on the feeding habits in nature of some ubiquitous taxa that are usually the most abundant. Particularly, these include cyclopoid copepods, nauplii of almost all types of copepods, and tintinnids and other ciliates. The same applies to other taxa such as marine cladocerans, appendicularians, thaliaceans, and various types of meroplankters which, although less ubiquitously abundant, exhibit sporadic and localized population increases. Limited information suggests that the trophodynamic impact of such population pulses can be substantial (Seki 1973; Wiebe et al. 1979).

In conclusion, I return to the thesis presented in the introduction, namely that understanding of fishery dynamics requires understanding of the dynamics of food webs supporting larval fish. Sandwiched between a need to understand responses of planktonic primary producers to climatic, oceanographic, and

anthropogenic-induced variability, and a need to understand trophic interactions between larval fish and their prey, is a critical need to understand dynamics and patterns of zooplankton feeding.

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Appendix Table 1.—Species of fish whose larvae have been reported to eat copepod nauplii.

Fish species	Reference
CLUPEIFORMES	
Anchoa mitchelli	Detwyler and Houde (1970)
Brevoortia patronus	Govoni et al. (1983)
B. tyrannus	Kjelson et al. (1975)
Clupea harengus	Bainbridge and Forsyth (1971)
Clupea harengus	Bjørke (1971, 1978)
Clupea harengus	Bowers and Williamson (1951)
Clupea harengus	Gamble et al. (1981)
Clupea harengus	Lebour (1918, 1919, 1920, 1921)
Clupea harengus	Ogilvie (1927)
Clupea harengus	Sherman and Honey (1971)
Engraulis anchoita	Ciechomski (1967)
E. mordax	Arthur (1976)
E. ringens	Mendiola (1974)
Harengula pensacolae	Detwyler and Houde (1970)
Sardina pilchardus	Lebour (1920, 1921)
Sardinops sagax	Arthur (1976)
Sprattus sprattus	Lebour (1918, 1921)
PERCIFORMES	
Ammodytes americanus	Covill (1959)
A. marinus	Ryland (1964)
A. marinus	Wyatt (1974)
A. tobianus	Lebour (1918, 1919, 1920)
Auxis sp.	Uotani et al. (1981)
Callionymus lyra	Lebour (1920)
Ctenolabrus rupestris	Lebour (1920)
Eutrigla gurnardus	Lebour (1920)
Gobius niger	Lebour (1920)
Gobiusculus flavescens	Lebour (1918, 1920)
Katsuwonus pelamis	Uotani et al. (1981)
Labrus bergylta	Lebour (1918, 1919, 1920)
L. bimaculatus	Lebour (1920)
Lagodon rhomboides	Kjelson et al. (1975)
Leiostomus xanthurus	Govoni et al. (1983)
Leiostomus xanthurus	Kjelson et al. (1975)
Lepadogaster candollei	Lebour (1918, 1920)
L. lepadogaster	Lebour (1918)
Micropogonias undulatus	Govoni et al. (1983)
Myoxocephalus aenaeus	Laroche (1982)
M. octodecemspinosus	Laroche (1982)
M. scorpius	Laroche (1982)
Pomatoschistus microps	Lebour (1920)
Sebastes marinus	Marak (1974)
Scomber scomber	Lebour (1918, 1920)
Thunnus alalunga	Uotani et al. (1981)
T. albacares	Uotani et al. (1981)
T. maccoyii	Uotani et al. (1981)
T. obesus	Uotani et al. (1981)
Trachinus vipera	Lebour (1918, 1919, 1920)
Trachurus symmetricus	Arthur (1976)
T. trachurus	Lebour (1920)
Triglops murrayi	Laroche (1982)
PLEURONECTIFORMES	
Limanda limanda	Last (1978a)
Limanda limanda	Lebour (1920)
Microstomus kitt	Lebour (1920)
Phrynorhombus norvegicus	Lebour (1918, 1920)
Platichthys flessus	Last (1978a)
Pleuronectes platessa	Last (1978a)
Pleuronectes platessa	Ryland (1964)
Pleuronectes platessa	Shelbourne (1953)
Pleuronectes platessa	Wyatt (1974)
Psetta maxima	Lebour (1920)
Pseudopleuronectes americanus	Pearcy (1962)
Scophthalmus maximus	Last (1979)
S. rhombrus	Lebour (1920)
Solea solea	Last (1978a)
GADIFORMES	
Ciliata mustela	Lebour (1918, 1920)
Gadus morhua	Ellertsen et al. (1981); Last (1978b); Marak (1960); Sysoeva and Degtereva (1965)
Melanogrammus aeglefinus	Marak (1960)
Melanogrammus aeglefinus	Ogilvie (1938)
Merlangius merlangus	Last (1978b)
Merlangius merlangus	Lebour (1918, 1919, 1920)
Merluccius merluccius	Lebour (1920)
M. productus	Sumida and Moser (1980)
Micromesistius poutassou	Conway (1980)
Molva molva	Lebour (1920)
Pollachius virens	Marak (1960)
Trisopterus luscus	Last (1978b)

Appendix Table 2.—Species of fish whose larvae have been reported to eat species of *Acartia*.

Fish species	Reference
CLUPEIFORMES	
Anchoa mitchelli	Detwyler and Houde (1970)
Brevoortia patronus	Govoni et al. (1983)
B. tyrannus	June and Carlson (1971)
B. tyrannus	Kjelson et al. (1975)
Clupea harengus	Bowers and Williamson (1951)
Clupea harengus	Gamble et al. (1981)
Clupea harengus	Lebour (1920, 1921)
Clupea harengus	Sherman and Honey (1971)
Harengula pensacolae	Detwyler and Houde (1970)
Sardina pilchardus	Lebour (1920, 1921)
PERCIFORMES	
Ammodytes americanus	Covill (1959)
A. tobianus	Lebour (1918, 1920)
Callionymus lyra	Lebour (1919, 1920)
Coryphoblennius galerita	Lebour (1919)
Cyclogaster montagui	Lebour (1919)
Gobius niger	Lebour (1918, 1919, 1920)
Gobiusculus flavescens	Lebour (1918, 1919, 1920)
Labrus bergylta	Lebour (1919, 1920)
Lagodon rhomboides	Kjelson et al. (1975)
Leiostomus xanthurus	Govoni et al. (1983)
Leiostomus xanthurus	Kjelson et al. (1975)
Micropogonias undulatus	Govoni et al. (1983)
Pomatoschistus microps	Lebour (1918, 1919, 1920)
Thunnus albacares	Uotani et al. (1981)
Trachurus trachurus	Lebour (1920)
PLEURONECTIFORMES	
Limanda limanda	Lebour (1920)
Microchirus variegatus	Lebour (1918)
Phrynorhombus norvegicus	Lebour (1918, 1920)
Platichthys flessus	Lebour (1920)
Scophthalmus maximus	Last (1979)
Solea nasuta	Lebour (1920)
Zeugopterus punctatus	Lebour (1920)
GADIFORMES	
Ciliata mustela	Lebour (1920)
Gadus morhua	Sysoeva and Degtereva (1965)
Melanogrammus aeglefinus	Ogilvie (1938)
Merlangius merlangus	Last (1978b)
Merlangius merlangus	Lebour (1919, 1920)
Micromesistius poutassou	Conway (1980)
Pollachius pollachius	Lebour (1918, 1919, 1920)
Trisopterus luscus	Last (1978b)
Trisopterus luscus	Lebour (1918, 1920)
T. minutus	Lebour (1918, 1920)

Appendix Table 3.—Species of fish whose larvae have been reported to eat species of *Calanus*.

Fish species	Reference
CLUPEIFORMES	
Clupea harengus	Blaxter (1965)
Clupea harengus	Bowers and Williamson (1951)
Clupea harengus	Gamble et al. (1981)
Clupea harengus	Ogilvie (1927)
Engraulis ringens	Mendiola (1974)
PERCIFORMES	
Auxis sp.	Uotani et al. (1981)
Callionymus lyra	Lebour (1918)
Crystallogobius nilssoni	Lebour (1918)
Eutrigla gurnardus	Lebour (1920)
Sebastes marinus	Bainbridge (1965)
Sebastes marinus	Marak (1974)
Thunnus obesus	Uotani et al. (1981)
Trachurus trachurus	Lebour (1918, 1920)
PLEURONECTIFORMES	
Arnoglossus sp.	Lebour (1920)
Limanda limanda	Lebour (1920)
Phrynorhombus norvegicus	Lebour (1918, 1920)
Zeugopterus punctatus	Lebour (1918)
GADIFORMES	
Gadus morhua	Lebour (1918)
Gadus morhua	Sysoeva and Degtereva (1965)
Melanogrammus aeglefinus	Ogilvie (1938)
Melanogrammus aeglefinus	Marak (1960)
Merlangius merlangus	Lebour (1919, 1920)
Merluccius merluccius	Lebour (1920)
M. productus	Sumida and Moser (1980)
Micromesistius poutassou	Conway (1980)
Pollachius pollachius	Lebour (1919, 1920)
P. virens	Marak (1960)
Trisopterus luscus	Lebour (1919, 1920)
T. minutus	Lebour (1920)

Appendix Table 4.—Species of fish whose larvae have been reported to eat species of *Centropages*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		PLEURONECTIFORMES	
Brevoortia tyrannus	June and Carlson (1971)	*Arnoglossus* sp.	Lebour (1920)
Brevoortia tyrannus	Kjelson et al. (1975)	*Psetta maxima*	Lebour (1918)
Clupea harengus	Lebour (1921)	*Scophthalmus maximus*	Last (1979)
Clupea harengus	Ogilvie (1927)	*S. rhombrus*	Lebour (1918)
Engraulis anchoita	Ciechomski (1967)	GADIFORMES	
PERCIFORMES		*Melanogrammus aeglefinus*	Ogilvie (1938)
Ammodytes tobianus	Lebour (1920)	*Melanogrammus aeglefinus*	Marak (1960)
Callionymus lyra	Lebour (1918)	*Merlangius merlangus*	Lebour (1920)
Lagodon rhomboides	Kjelson et al. (1975)	*Micromesistius poutassou*	Conway (1980)
Leiostomus xanthurus	Kjelson et al. (1975)	*Pollachius virens*	Marak (1960)
Lepadogaster lepadogaster	Lebour (1918)		
Sebastes marinus	Marak (1974)		
Trachurus trachurus	Lebour (1918, 1920)		

Appendix Table 5.—Species of fish whose larvae have been reported to eat species of *Paracalanus*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		PLEURONECTIFORMES	
Brevoortia patronus	Govoni et al. (1983)	*Arnoglossus* sp.	Lebour (1918)
Clupea harengus	Bowers and Williamson (1951)	*Phrynorhombus norvegicus*	Lebour (1918, 1920)
Clupea harengus	Lebour (1920, 1921)	*P. regias*	Lebour (1918)
Clupea harengus	Ogilvie (1927)	GADIFORMES	
Engraulis anchoita	Ciechomski (1967)	*Gadus morhua*	Last (1978b)
PERCIFORMES		*Melanogrammus aeglefinus*	Marak (1960)
Ammodytes americanus	Covill (1959)	*Melanogrammus aeglefinus*	Ogilvie (1938)
A. tobianus	Lebour (1920)	*Merlangius merlangus*	Last (1978b)
Auxis sp.	Uotani et al. (1981)	*Merlangius merlangus*	Lebour (1918, 1920)
Callionymus lyra	Lebour (1918, 1920)	*Merluccius productus*	Sumida and Moser (1980)
Eutrigla gurnardus	Lebour (1920)	*Molva molva*	Lebour (1920)
Gobiusculus flavescens	Lebour (1920)	*Pollachius virens*	Marak (1960)
Labrus bergylta	Lebour (1920)	*Trisopterus luscus*	Last (1978b)
L. bimaculatus	Lebour (1920)		
Leiostomus xanthurus	Govoni et al. (1983)		
Micropogonias undulatus	Govoni et al. (1983)		
Thunnus alalunga	Uotani et al. (1981)		
T. albacares	Uotani et al. (1981)		
T. maccoyii	Uotani et al. (1981)		
T. obesus	Uotani et al. (1981)		
Trachurus trachurus	Lebour (1920)		

Appendix Table 6.—Species of fish whose larvae have been reported to eat species of *Pseudocalanus*.

Fish species	Reference
CLUPEIFORMES	
Clupea harengus	Bowers and Williamson (1951)
Clupea harengus	Gamble et al. (1981)
Clupea harengus	Lebour (1918, 1919, 1920, 1921)
Clupea harengus	Ogilvie (1927)
Clupea harengus	Sherman and Honey (1971)
Sardina pulchardus	Lebour (1920, 1921)
Sprattus sprattus	Lebour (1918, 1921)
PERCIFORMES	
Agonus cataphractus	Lebour (1920)
Ammodytes americanus	Covill (1959)
A. marinus	Ryland (1964)
A. tobianus	Lebour (1918, 1919, 1920)
Callionymus lyra	Lebour (1918, 1919, 1920)
Eutrigla gurnardus	Lebour (1920)
Gobius niger	Lebour (1919, 1920)
Gobiusculus flavescens	Lebour (1918, 1919, 1920)
Labrus bergylta	Lebour (1918)
L. bimaculatus	Lebour (1920)
Lepadogaster candollei	Lebour (1919, 1920)
L. lepadogaster	Lebour (1918)
Myoxocephalus scorpius	Laroche (1982)
Pomatoschistus microps	Lebour (1919, 1920)
Sebastes marinus	Marak (1974)
Taurulus bubalis	Lebour (1919, 1920)
Trachinus vipera	Lebour (1918, 1919, 1920)
Trachurus trachurus	Lebour (1920)
Triglops murrayi	Laroche (1982)
PLEURONECTIFORMES	
Arnoglossus sp.	Lebour (1918, 1919, 1920)
Limanda limanda	Last (1978a)
Limanda limanda	Lebour (1918, 1920)
Microchirus variegatus	Lebour (1918)
Phrynorhombus norvegicus	Lebour (1918, 1920)
P. regias	Lebour (1918)
Pleuronectes platessa	Ryland (1964)
Psetta maxima	Lebour (1920)
Scophthalmus maximus	Last (1979)
Solea nasuta	Lebour (1920)
GADIFORMES	
Gadus morhua	Last (1978b)
Gadus morhua	Marak (1960)
Gadus morhua	Sysoeva and Degtereva (1965)
Melanogrammus aeglefinus	Marak (1960)
Melanogrammus aeglefinus	Ogilvie (1938)
Merlangius merlangus	Last (1978b)
Merlangius merlangus	Lebour (1918, 1919, 1920)
Merluccius merluccius	Lebour (1920)
Micromesistius poutassou	Conway (1980)
Molva molva	Lebour (1920)
Pollachius pollachius	Lebour (1919)
P. virens	Marak (1960)
Trisopterus luscus	Last (1978b)
Trisopterus luscus	Lebour (1918, 1919, 1920)
T. minutus	Lebour (1918, 1920)

Appendix Table 7.—Species of fish whose larvae have been reported to eat species of *Temora*.

Fish species	Reference
CLUPEIFORMES	
Brevoortia patronus	Govoni et al. (1983)
B. tyrannus	June and Carlson (1971)
B. tyrannus	Kjelson et al. (1975)
Clupea harengus	Gamble et al. (1981)
Clupea harengus	Ogilvie (1927)
Sardina pilchardus	Lebour (1921)
PERCIFORMES	
Agonus cataphractus	Lebour (1920)
Ammodytes americanus	Covill (1959)
A. tobianus	Lebour (1920)
Callionymus lyra	Lebour (1918, 1919, 1920)
Coryphoblennius galerita	Lebour (1918)
Crystallogobius nilssoni	Lebour (1920)
Ctenolabrus rupestris	Lebour (1919, 1920)
Cyclogaster montagui	Lebour (1919)
Diplecogaster bimaculatus	Lebour (1920)
Eutrigla gurnardus	Lebour (1920)
Gobius niger	Lebour (1919)
Gobiusculus flavescens	Lebour (1918, 1919)
Labrus bergylta	Lebour (1918, 1919, 1920)
L. bimaculatus	Lebour (1920)
Lagodon rhomboides	Kjelson et al. (1975)
Leiostomus xanthurus	Govoni et al. (1983)
Leiostomus xanthurus	Kjelson et al. (1975)
Lepadogaster candollei	Lebour (1918, 1919, 1920)
Micropogonias undulatus	Govoni et al. (1983)
Myoxocephalus aenaeus	Laroche (1982)
M. octodecemspinosus	Laroche (1982)
M. scorpius	Laroche (1982)
Pomatoschistus microps	Lebour (1920)
Scomber scomber	Lebour (1920)
Taurulus bubalis	Lebour (1918, 1919, 1920)
Trachinus vipera	Lebour (1919, 1920)
Trachurus trachurus	Lebour (1919, 1920)
Triglops murrayi	Laroche (1982)
PLEURONECTIFORMES	
Limanda limanda	Last (1978a)
Limanda limanda	Lebour (1918, 1920)
Microchirus variegatus	Lebour (1918)
Phrynorhombus norvegicus	Lebour (1918, 1920)
P. regias	Lebour (1918)
Platichthys flessus	Lebour (1920)
Pleuronectes platessa	Last (1978a)
Pleuronectes platessa	Lebour (1918, 1920)
Psetta maxima	Lebour (1918)
Scophthalmus maximus	Last (1979)
S. rhombrus	Lebour (1918, 1920)
Solea nasuta	Lebour (1918, 1920)
S. solea	Lebour (1918)
Zeugopterus punctatus	Lebour (1918, 1920)
GADIFORMES	
Ciliata mustela	Lebour (1919)
Gadus morhua	Lebour (1918)
Melanogrammus aeglefinus	Marak (1960)
Melanogrammus aeglefinus	Ogilvie (1938)
Merlangius merlangus	Last (1978b)
Merlangius merlangus	Lebour (1919, 1920)
Pollachius pollachius	Lebour (1918, 1919, 1920)
P. virens	Marak (1960)
Trisopterus luscus	Lebour (1920)
T. minutus	Lebour (1920)

Appendix Table 8.—Species of fish whose larvae have been reported to eat species of *Corycaeus*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		*Trachurus symmetricus*	Arthur (1976)
Brevoortia patronus	Govoni et al. (1983)	*T. trachurus*	Lebour (1920)
Clupea harengus	Lebour (1918, 1920, 1921)	*Thunnus alalunga*	Uotani et al. (1981)
Engraulis anchoita	Ciechomski (1967)	*T. albacares*	Uotani et al. (1981)
PERCIFORMES		*T. maccoyii*	Uotani et al. (1981)
Callionymus lyra	Lebour (1918)	*T. obesus*	Uotani et al. (1981)
Katsuwonus pelamis	Uotani et al. (1981)	PLEURONECTIFORMES	
Leiostomus xanthurus	Govoni et al. (1983)	*Limanda limanda*	Lebour (1918)
Micropogonias undulatus	Govoni et al. (1983)	*Microchirus variegata*	Lebour (1918)
Trachinus vipera	Lebour (1919)	*Scophthalmus norvegicus*	Lebour (1918)

Appendix Table 9.—Species of fish whose larvae have been reported to eat species of *Oithona*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		*Sebastes marinus*	Bainbridge (1965)
Brevoortia patronus	Govoni et al. (1983)	*Sebastes marinus*	Marak (1974)
B. tyrannus	Kjelson et al. (1975)	*Thunnus alalunga*	Uotani et al. (1981)
Clupea harengus	Bowers and Williamson (1951)	*T. maccoyii*	Uotani et al. (1981)
Clupea harengus	Gamble et al. (1981)	*Trachinus vipera*	Lebour (1919)
Clupea harengus	Lebour (1918, 1920)	*Trachurus symmetricus*	Arthur (1976)
Clupea harengus	Ogilvie (1927)	*T. trachurus*	Lebour (1920)
Clupea harengus	Sherman and Honey (1971)	PLEURONECTIFORMES	
Engraulis anchoita	Ciechomski (1967)	*Phrynorhombus norvegicus*	Lebour (1920)
Sardina pilchardus	Lebour (1920, 1921)	GADIFORMES	
PERCIFORMES		*Ciliata mustella*	Lebour (1919)
Ammodytes americanus	Covill (1959)	*Gadus morhua*	Sysoeva and Degtereva (1965)
A. tobianus	Lebour (1918, 1919, 1920)	*Melanogrammus aeglefinus*	Ogilvie (1938)
Labrus bergylta	Lebour (1920)	*Merlangius merlangus*	Lebour (1920)
L. bimaculatus	Lebour (1920)	*Merluccius productus*	Sumida and Moser (1980)
Lagodon rhomboides	Kjelson et al. (1975)	*Micromesistius poutassou*	Conway (1980)
Leiostomus xanthurus	Govoni et al. (1983)	*Pollachius pollachius*	Lebour (1919, 1920)
Leiostomus xanthurus	Kjelson et al. (1975)		
Micropogonias undulatus	Govoni et al. (1983)		
Pomatoschistus microps	Lebour (1920)		

Appendix Table 10.—Species of fish whose larvae have been reported to eat species of *Oncaea*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		PLEURONECTIFORMES	
Brevoortia patronus	Govoni et al. (1983)	*Microchirus variegatus*	Lebour (1918)
Clupea harengus	Lebour (1918)	*Phrynorhombus norvegicus*	Lebour (1918)
PERCIFORMES		*Solea vulgaris*	Lebour (1918)
Leiostomus xanthurus	Govoni et al. (1983)	*Zeugopterus punctatus*	Lebour (1918)
Micropogonias undulatus	Govoni et al. (1983)	GADIFORMES	
Trachurus symmetricus	Arthur (1976)	*Merlangius merlangus*	Lebour (1918)
		Micromesistius poutassou	Conway (1980)

Appendix Table 11.—Species of fish whose larvae have been reported to eat species of *Euterpina*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		*Limanda limanda*	Lebour (1918)
Brevoortia patronus	Govoni et al. (1983)	*Microchirus variegatus*	Lebour (1918)
Clupea harengus	Lebour (1918)	*Microstomus kitt*	Lebour (1918)
Engraulis anchoita	Ciechomski (1967)	*Phrynorhombus norvegicus*	Lebour (1918)
PERCIFORMES		*P. regias*	Lebour (1918)
Callionymus lyra	Lebour (1918)	*Solea nasuta*	Lebour (1918)
Labrus bergylta	Lebour (1918)	*S. solea*	Lebour (1918)
PLEURONECTIFORMES		*Zeugopterus punctatus*	Lebour (1918)
Arnoglossus sp.	Lebour (1918)	GADIFORMES	
		Ciliata mustella	Lebour (1919)
		Pollachius pollachius	Lebour (1918)
		Trisopterus minutus	Lebour (1918)

Appendix Table 12.—Species of fish whose larvae have been reported to eat species of *Microsetella*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		PLEURONECTIFORMES	
Brevoortia patronus	Govoni et al. (1983)	*Microchirus variegatus*	Lebour (1918)
Clupea harengus	Bjorke (1971, 1978)	*Solea solea*	Last (1978a)
Clupea harengus	Ogilvie (1927)	GADIFORMES	
PERCIFORMES		*Micromesistius poutassou*	Conway (1980)
Leiostomus xanthurus	Govoni et al. (1983)		
Micropogonias undulatus	Govoni et al. (1983)		
Myoxocephalus aenaeus	Laroche (1982)		
M. octodecemspinosus	Laroche (1982)		
M. scorpius	Laroche (1982)		
Trachurus symmetricus	Arthur (1976)		

Appendix Table 13.—Species of fish whose larvae have been reported to eat other (mostly unidentified) harpacticoid copepods.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		*Lepadogaster condollei*	Lebour (1918, 1919, 1920)
Brevoortia patronus	Govoni et al. (1983)	*L. lepadogaster*	Lebour (1918)
B. tyrannus	Kjelson et al. 1975)	*Micropogonias undulatus*	Govoni et al. (1983)
Clupea harengus	Bowers and Williamson (1951)	*Myoxocephalus undulatus*	Laroche (1982)
Clupea harengus	Gamble et al. (1981)	*M. octodecemspinosus*	Laroche (1982)
Clupea harengus	Lebour (1918, 1920, 1921)	*M. scorpius*	Laroche (1982)
Clupea harengus	Ogilvie (1927)	*Trachurus symmetricus*	Arthur (1976)
Clupea harengus	Sherman and Honey (1971)	*Triglops murrayi*	Laroche (1982)
Sardina pilchardus	Lebour (1921)	PLEURONECTIFORMES	
Sprattus sprattus	Lebour (1921)	*Limanda limanda*	Lebour (1920)
PERCIFORMES		*Microchirus variegatus*	Lebour (1918)
Agonus cataphractus	Lebour (1920)	*Pseudopleuronectes americanus*	Pearcy (1962)
Callionymus lyra	Lebour (1919)	*Solea solea*	Lebour (1918)
Ctenolabrus rupestris	Lebour (1920)	GADIFORMES	
Diplecogaster bimaculatus	Lebour (1919)	*Melanogrammus aeglefinus*	Ogilvie (1938)
Gobius niger	Lebour (1919)	*Merlangius merlangus*	Lebour (1920)
Gobiusculus flavescens	Lebour (1919, 1920)	*Pollachius pollachius*	Lebour (1919, 1920)
Labrus bergylta	Lebour (1919, 1920)	*Trisopterus luscus*	Lebour (1920)
L. bimaculatus	Lebour (1920)		
Lagodon rhomboides	Kjelson et al. (1975)		
Leiostomus xanthurus	Govoni et al. (1983)		
Leiostomus xanthurus	Kjelson et al. (1975)		

Appendix Table 14.—Species of fish whose larvae have been reported to eat tintinnids.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		PLEURONECTIFORMES	
Anchoa mitchelli	Detwyler and Houde (1970)	*Limanda limanda*	Last (1978a)
Brevoortia patronus	Govoni et al. (1983)	*Limanda limanda*	Lebour (1918)
Clupea harengus	Bainbridge and Forsyth (1971)	*Microchirus variegatus*	Lebour (1918)
Clupea harengus	Lebour (1920, 1921)	*Phrynorhombus norvegicus*	Lebour (1918)
Clupea harengus	Sherman and Honey (1971)	*Platichthys flessus*	Last (1978a)
Engraulis mordax	Arthur (1976)	*Pseudopleuronectes americanus*	Pearcy (1962)
E. ringens	Mendiola (1974)	GADIFORMES	
Sardinops sagax	Arthur (1976)	*Gadus morhua*	Last (1978b)
Sprattus sprattus	Lebour (1921)	*Melanogrammus aeglefinus*	Ogilvie (1938)
PERCIFORMES		*Merlangius merlangus*	Last (1978b)
Leiostomus xanthurus	Govoni et al. (1983)	*Micromesistius poutassou*	Conway (1980)
Micropogonias undulatus	Govoni et al. (1983)	*Trisopterus luscus*	Last (1978b)
Trachurus symmetricus	Arthur (1976)		

Appendix Table 15.—Species of fish whose larvae have been reported to eat species of *Evadne*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		PLEURONECTIFORMES	
Clupea harengus	Lebour (1918, 1921)	*Scophthalmus maximus*	Last (1979)
Clupea harengus	White (1980)	*Solea solea*	Lebour (1918)
Engraulis anchoita	Ciechomski (1967)	GADIFORMES	
PERCIFORMES		*Gadus morhua*	Sysoeva and Degtereva (1965)
Auxis sp.	Uotani et al. (1981)	*Melanogrammus aeglefinus*	Marak (1960)
Katsuwonus pelamis	Uotani et al. (1981)	*Melanogrammus aeglefinus*	Ogilvie (1938)
Leiostomus xanthurus	Govoni et al. (1983)	*Micromesistius poutassou*	Conway (1980)
Lepadogaster condollei	Lebour (1920)		
Scomber scomber	Lebour (1920)		
Thunnus alalunga	Uotani et al. (1981)		
T. albacares	Uotani et al. (1981)		
T. maccoyii	Uotani et al. (1981)		
T. obesus	Uotani et al. (1981)		
Trachinus vipera	Lebour (1920)		

Appendix Table 16.—Species of fish whose larvae have been reported to eat species of *Podon*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		PLEURONECTIFORMES	
Clupea harengus	Ogilvie (1927)	*Limanda limanda*	Lebour (1918, 1920)
Engraulis anchoita	Ciechomski (1967)	*Microchirus variegatus*	Lebour (1918)
PERCIFORMES		*Phrynorhombus norvegicus*	Lebour (1918, 1920)
Ammodytes tobianus	Lebour (1919)	*P. regias*	Lebour (1918)
Blennius gattorugine	Lebour (1918, 1919)	*Psetta maxima*	Lebour (1920)
Callionymus lyra	Lebour (1918, 1920)	*Scophthalmus maximus*	Last (1979)
Coryphoblennius galerita	Lebour (1919)	*S. rhombrus*	Lebour (1918)
Crystallogobius nilssoni	Lebour (1918)	GASIFORMES	
Ctenolabrus rupestris	Lebour (1920)	*Melanogrammus aeglefinus*	Ogilvie (1938)
Diplecogaster bimaculatus	Lebour (1920)	*Merlangius merlangus*	Lebour (1920)
Eutrigla gurnardus	Lebour (1918, 1920)	*Micromesistius poutassou*	Conway (1980)
Gobiusculus flavescens	Lebour (1919)	*Molva molva*	Lebour (1920)
Labrus bergylta	Lebour (1918, 1919, 1920)	*Pollachius pollachius*	Lebour (1920)
L. bimaculatus	Lebour (1920)	*Trisopterus luscus*	Lebour (1920)
Lepadogaster candollei	Lebour (1919, 1920)	*T. minutus*	Lebour (1918, 1920)
Scomber scomber	Lebour (1920)		
Trachinus vipera	Lebour (1920)		
Trachurus trachurus	Lebour (1920)		

Appendix Table 17.—Species of fish whose larvae have been reported to eat barnacle nauplii.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		*Leiostomus xanthurus*	Kjelson et al. (1975)
Brevoortia patronus	Govoni et al. (1983)	*Micropogonias undulatus*	Govoni et al. (1983)
B. tyrannus	Kjelson et al. (1975)	*Myoxocephalus aenaeus*	Laroche (1982)
Clupea harengus	Bjørke (1978)	*M. octodecemspinosus*	Laroche (1982)
Clupea harengus	Lebour (1918, 1920, 1921)	*M. scorpius*	Laroche (1982)
Clupea harengus	Ogilvie (1927)	*Pomatoschistus microps*	Lebour (1920)
Clupea harengus	Sherman and Honey (1971)	*Taurulus bubalis*	Lebour (1918, 1919, 1920)
Harengula pensacolae	Detwyler and Houde (1970)	*Triglops murrayi*	Laroche (1982)
PERCIFORMES		PLEURONECTIFORMES	
Agonus cataphractus	Lebour (1919, 1920)	*Psetta maxima*	Lebour (1918)
Callionymus lyra	Lebour (1918)	*Solea solea*	Lebour (1918)
Diplecogaster bimaculatus	Lebour (1919, 1920)	GADIFORMES	
Gobiusculus flavescens	Lebour (1919)	*Merlangius merlangus*	Lebour (1919, 1920)
Labrus bergylta	Lebour (1919, 1920)		
Lagodon rhomboides	Kjelson et al. (1975)		

Appendix Table 18.—Species of fish whose larvae have been reported to eat gastropod larvae.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		PLEURONECTIFORMES	
Anchoa mitchelli	Detwyler and Houde (1970)	*Limanda limanda*	Lebour (1920)
Clupea harengus	Bowers and Williamson (1951)	*Pleuronectes platessa*	Shelbourne (1953)
Clupea harengus	Gamble et al. (1981)	*Scophthalmus maximus*	Last (1979)
Clupea harengus	Lebour (1918, 1920, 1921)	*Solea solea*	Last (1978a)
Clupea harengus	Ogilvie (1927)	GADIFORMES	
Engraulis mordax	Lasker et al. (1970)	*Ciliata mustela*	Lebour (1920)
Sprattus sprattus	Lebour (1919, 1921)	*Melanogrammus aeglefinus*	Marak (1960)
PERCIFORMES		*Melanogrammus aeglefinus*	Ogilvie (1938)
Ammodytes tobianus	Lebour (1920)	*Micromesistius poutassou*	Conway (1980)
Diplecogaster bimaculatus	Lebour (1919)	*Pollachius pollachius*	Lebour (1920)
Gobiusculus flavescens	Lebour (1919, 1920)		
Labrus bergylta	Lebour (1920)		
Lepadogaster lepadogaster	Lebour (1919)		
Pomatoschistus microps	Lebour (1919)		
Scomber scomber	Lebour (1918)		
Taurulus bubalis	Lebour (1918, 1919)		
Trachurus trachurus	Lebour (1920)		

Appendix Table 19.—Species of fish whose larvae have been reported to eat species of *Limacina*.

Fish species	Reference	Fish species	Reference
CLUPEIFORMES		GADIFORMES	
Brevoortia patronus	Govoni et al. (1983)	*Melanogrammus aeglefinus*	Ogilvie (1938)
Clupea harengus	White (1977)	*Micromesistius poutassou*	Conway (1980)
Engraulis mordax	Arthur (1976)		
Sardinops sagax	Arthur (1976)		
PERCIFORMES			
Leiostomus xanthurus	Govoni et al. (1983)		
Micropogonias undulatus	Govoni et al. (1983)		

Appendix Table 20.—Species of fish whose larvae have been reported to eat appendicularians.

Fish species	Reference	Fish species	Reference
PERCIFORMES		PLEURONECTIFORMES	
Ammodytes marinus	Ryland (1964)	*Limanda limanda*	Last (1978a)
Ammodytes marinus	Wyatt (1974)	*Platichthys flessus*	Last (1978a)
Auxis sp.	Uotani et al. (1981)	*Pleuronectes platessa*	Last (1978a)
Katsuwonus pelamis	Uotani et al. (1981)	*Pleuronectes platessa*	Ryland (1964)
Thunnus alalunga	Uotani et al. (1981)	*Pleuronectes platessa*	Shelbourne (1953, 1957, 1962)
T. albacares	Uotani et al. (1981)		
T. maccoyii	Uotani et al. (1981)	*Pleuronectes platessa*	Wyatt (1974)
T. obesus	Uotani et al. (1981)	*Scophthalmus maximus*	Last (1979)
		GADIFORMES	
		Micromesistius poutassou	Conway (1980)

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